

MASS COLLECTIONS: RUBUS ODORATUS AND R. PARVIFLORUS

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In 1938 a grant was made by the Wisconsin Alumni Research Foundation for the study of the so-called preglacial relics in the flora of the upper Great Lakes region. This study was eventually narrowed to one species, the Thimbleberry or Salmonberry (*Rubus parviflorus*), whose range shows a gap between Lake Superior and the Black Hills of South Dakota which has been interpreted as due to survival on nunataks about Lakes Superior and Huron. Funds from the estate of the late Dr. J. J. Davis, made available through the generosity of his daughter, Miss Marguerite Davis, made it possible for the writer to carry on this study in the summer of 1939, when the species was collected in South Dakota, Wyoming, Utah and Colorado. Friends in California, Alberta, Wisconsin, Oregon, Colorado, Indiana, New York, Montana and South Dakota have also contributed collections; their names are cited with their collections in tables I and V, and grateful acknowledgement is here made for their assistance, without which this study would not have been possible.

The method used was different from ordinary taxonomic or

Issued September 20, 1941.

ecological techniques: it consisted of collecting many individuals from each colony of Thimbleberry and determining in the laboratory the percentage of plants showing each character. By comparing figures from different regions it has been possible to judge their closeness of relationship; also, some taxonomic changes have been indicated. It became evident that results concerning a plant with a disrupted range like that of *R. parviflorus* were difficult to evaluate in absence of a similar study of a species with an essentially continuous range; accordingly, mass collections were made, in 1938-40, of the eastern *R. odoratus*. Findings in this species will be considered first.

In assembling the distributional data in Maps 12, 24 and 27, the writer is indebted to many friends for assistance; these include Mr. H. D. House, Dr. Earl Core, Dr. T. M. C. Taylor, Dr. J. M. Fogg, Jr., Dr. F. T. McFarland, Dr. E. Lucy Braun, Dr. R. M. Harper, Dr. A. J. Sharp, Dr. F. K. Butters and Dr. Hugh Raup. Maps 10, 12, 19, 20, 21, 24, 25, 26, and 29-34 were prepared from base maps of Hall's 'Outline Maps and Graphs,' published by permission of the author and publisher, John Wiley & Sons, Inc. Maps 35 and 36 are (except for botanical data) from map by Erwin Raisz in Atwood's 'The Physiographic Provinces of North America,' courtesy of Ginn & Co. Professor Walter Cottam, of the University of Utah, has most kindly supplied figs. 5, 6 and 7 of pls. 11 and 12.

I. VARIATION IN *R. odoratus*

1. THE KINDS OF VARIATION

Rubus odoratus, ranging from Nova Scotia and Quebec to Michigan, and southward to Georgia and Tennessee, shows variations which are to a great extent the exact counterparts of those which were described as varieties in *R. parviflorus*.¹ The two pairs of characters (leaves soft-pubescent beneath *vs.* glabrous or glabrate beneath, and pedicels with long-stalked glands *vs.* short-stalked glands) which recombine to make the four "varieties" of *R. parviflorus*—*hypomalacus*, *heterade-*

¹ Fernald, *Rhodora* 37: 276. 1935.

nus, *bifarius* and *grandiflorus*—appear in just the same combinations in *R. odoratus*. Each of these four combinations ranges essentially throughout the range of the species, so they seem better treated as forms than as varieties.

As in *R. parviflorus*, the distinctions within each pair of characters are not always perfectly marked. Clearly glabrous leaves occur, as do extremely velvety ones, but some intermediates are as difficult to place as they occasionally are in the western species. Many plants have leaves which are appressed-pubescent and feel either harsh or velvety depending on how they happen to have been pressed. In some cases both surfaces are without doubt glabrate, the younger ones appearing densely velvety. In placing these questionable individuals recourse has been had to a character pointed out by Fernald²: truly velvety leaves ordinarily bear dark long-stalked glands on their upper surface. The correlation is good, but not perfect, through much of the range of the species. It breaks down completely in two large collections from the unglaciated part of Indiana; here, isolated from the rest of the range for a long time, the plants often have a different appearance (lighter colored, more glabrous and lustrous leaves), frequently carry on the leaves a type of gland not generally found on the species in other parts of the country, and, as has just been stated, lack the usual correlation of glandular upper surfaces with velvety lower surfaces.

The type of gland found mainly in Indiana is on the lower leaf-surfaces along the veins, and has a stalk 2–4 mm. long, which much exceeds those of other forms. Plants with long-stalked glands are not exclusively present in the collections from Indiana, but they outnumber plants with shorter glands.

A plant of very rare occurrence has the glands on the pedicels nearly sessile; this parallels *R. parviflorus* var. *scopulorum* and var. *parvifolius*.

Leaf shapes vary greatly in this species, but because of some variation even on single branches these characters are not as conveniently dealt with as are those of epidermal outgrowths. Examination of any good-sized collection will show singly-

² *Rhodora* 24: 175. 1922.

toothed and doubly-toothed margins, triangular lobes and oblong-triangular lobes, and depth of lobing varying from $\frac{1}{4}$ to $\frac{1}{2}$ the radius of the leaf. An individual with deeply lobed leaves has been described as *R. odoratus* var. *columbianus*,³ or *R. columbianus*.⁴

Sometimes the calyx is covered with a white felt-like tomentum; this proves to be due to the fungus infection *Sphaerotheca humuli*.

2. TAXONOMY OF INTRASPECIFIC VARIATION

To facilitate discussion of these six phases of *R. odoratus* and of the geographic occurrence of the characters on which they are based, it seems advisable to give them names. That the parallelism of five of them with variants of *R. parviflorus* may appear clearly, they are given names identical with or phonetically similar to those used in the more western species.

RUBUS ODORATUS L. f. **hypomalacus**, n.f., foliis subtus velutinis vel subvelutinis, supra fusco-glandulosis; pedicellorum glandulis stipitatis 1–3 mm. longis.—TYPE, in Herb. Univ. Wis.: roadcut, Ravine, Pa., July 11, 1940, *Fassett 20812*. (*R. odoratus* var. *malachophyllus* Fernald.)

R. ODORATUS f. **heteradenius**, n.f., foliis subtus glabris vel glabratibus vel sparse appresso-pilosis, supra eglandulosis; pedicellorum glandulis stipitatis 1–3 mm. longis.—TYPE, in Herb. Univ. Wis.: Wilmington Mountain, east of Bennington, Vt., Aug. 4, 1938, *Fassett 20787*.

R. ODORATUS f. **bifarius**, n.f., foliis subtus velutinis vel subvelutinis, supra fusco-glandulosis; pedicellorum glandulis stipitatis 0.5–1 mm. longis.—TYPE, in Herb. Univ. Wis.: cuts and fills along U. S. 6 west of Bear Mountain Bridge, N. Y., July 10, 1940, *Fassett 20806*.

R. ODORATUS f. **glabrifolius**, n.f., foliis subtus glabris vel glabratibus vel sparse appresso-pilosis, supra eglandulosis; pedicellorum glandulis stipitatis 0.5–1 mm. longis.—TYPE, in Herb. Univ. Wis.: woods and roadside banks 3 miles north of Vassalboro, Me., Aug. 16, 1939, *Fassett 20781*.

R. ODORATUS f. **scopulorum** n.f., foliis subtus glabris vel glabratibus vel sparse appresso-pilosis, supra eglandulosis; pedicellorum glandulis subsessilibus vel stipitatis non quaterlongioribus quam glandulis.—TYPE, in Herb. Univ. Wis.: roadcuts along U. S. 30, Sideling Hill, Pa.,

³ Millspaugh, Bull. W. Va. Exper. Stat. 2: 355. 1892.

⁴ Rydberg in Britton, Manual, p. 495. 1901.

July 11, 1940, *Fassett 20817*. The illustration of *R. parviflorus* var. *scopulorum*, in *Rhodora*, vol. 37, pl. 365, fig. 5, might well serve also as an illustration for *R. odoratus* f. *scopulorum*.

R. ODORATUS f. **parahypomalacus**, n.f., f. *hypomalacum* simulans, sed venis subtus glandulis 1-2 (-3) mm. longis.—TYPE, in Herb. Univ. Wis.: woods and cut-over land, foot of Shenandoah Mt., east of Franklin, W. Va., July 12, 1940, *Fassett 20823*.

R. ODORATUS f. **paraheteradenius**, n.f., f. *heteradenium* simulans, sed venis subtus glandulis 1-2(-3) mm. longis.—TYPE, in Herb. Univ. Wis.: along roadside, from halfway down to base of steep slope, associated with *Tsuga canadensis*, Guthrie Creek, about 2 miles east of Leesville, Ind., July, 1939, *R. M. Kreibel, C. F. McGraw & Morris Reeves*.

These forms may be keyed as follows:

- a. Pedicels with glands on stalks mostly 0.5 mm. or more long, the stalks more than 4 times as long as the gland
 - b. Stalks of glands on pedicels mostly more than 1 mm. long
 - c. Veins on lower leaf-surfaces with glands whose stalks are 0.2-1.0 mm. long
 - d. Leaves without dark-stalked glands on the upper surface, glabrous or lightly appressed-pubescent beneath.....f. *heteradenius*
 - d. Leaves with dark-stalked glands on the upper surface, more or less velvety beneath.....f. *hypomalacus*
 - c. Veins on lower leaf-surfaces with glands whose stalks are 1-2 (-3) mm. long
 - e. Leaves glabrous or glabrate or lightly appressed-pubescent beneath.....f. *paraheteradenius*
 - e. Leaves velvety beneath.....f. *parahypomalacus*
 - b. Stalks of glands on pedicels mostly 1 mm. or less long
 - f. Leaves with dark-stalked glands on the upper surface, more or less velvety beneath.....f. *bifarius*
 - f. Leaves without dark-stalked glands on the upper surface, glabrous or glabrate or lightly appressed-pubescent beneathf. *glabrifolius*
- a. Pedicels with glands subsessile or on stalks less than 0.5 mm. long and less than 4 times as long as the gland.....f. *scopulorum*

3. GEOGRAPHIC OCCURRENCE OF EACH FORM IN MASS COLLECTIONS

The object of this paper is not primarily to describe seven forms, or to point out the similarity of variation within *R. odoratus* to that within *R. parviflorus*. It is rather to study statistically the occurrence throughout the range of *R. odoratus* of each character used in the above key, and to determine what, if any, correlation there may be between the occurrence of these characters and the late geological history of the species.

For this purpose specimens have been taken from as many individuals as possible in each colony of the species which the writer has seen in the past three years; similar collections have also been made by several friends whose names appear in table I. The location of each mass collection is shown by a slanted figure on maps 1 and 2. It will be noted that in each state or province the numbers start anew. Table I gives the collection data for each collection, and table II the constituent forms of each.

TABLE I

MAINE: 1. Vassalboro, Aug. 16, 1939, 20781.⁵ 2. Augusta, Aug. 14, 1939, 20782. 3. Paris, Aug. 8, 1939, 20783. VERMONT: 1. Colchester, Aug. 7, 1939, 20785. 2.⁶ Burlington, Aug. 7, 1939, 20786. 3. Wilmington Mountain, Bennington, Aug. 4, 1938, 20787. 4. Wilmington Mountain, Bennington, Aug. 4, 1938, 20788. MASSACHUSETTS: 1. Near Cold River, east slope of Mohawk Trail, June 25, 1940, 20789. 2. West slope of Mohawk Trail below Hairpin Turn, June 25, 1940, 20790. ONTARIO: 1. West of Brockville, Aug. 7, 1939, 20791. NEW YORK: 1. Westfall Road, Penfield Township, Monroe Co., June 30, 1940, *R. E. Shanks*. 2. Atlantic Avenue, Penfield Township, June 30, 1940, *Shanks*. 3. Eaton Road, Irondequoit, Monroe Co., July 14, 1940, *Shanks*. 4. Pellett Road, Webster Township, Monroe Co., June 30, 1940, *Shanks*. 5. Watervliet, June 24, 1940, 20792. 6. Duanesburg, June 24, 1940, 20793. 7. Schenevus, June 24, 1940, 20794. 8. Chenango Bridge, June 24, 1940, 20795. 9. Woodhull, June 23, 1940, 20796. 10. Greenwood, June 23, 1940, 20797. 11. Bolivar, June 23, 1940, 20798. 12. North side of Allegheny River, 4 miles north of Limestone, June 23, 1940, 20799. 13. Three miles north of Limestone, June 23, 1940, 20800. 14. About a mile south of the Lake, Allegany State Park, June 21, 1940, 20801. 15. Quaker Bridge, June 21, 1940, 20802. 16. Allegany State Park, 5 miles west of Limestone, June 23, 1940, 20803. 17. Peekskill, July 10, 1940, 20804. 18. U. S. 6 east of Bear Mountain Bridge, July 10, 1940, 20805. 19. U. S. 6 west of Bear Mountain Bridge, July 10, 1940, 20806. 20. West Haverstraw, July 14, 1940, 20807. 21. Chester, July 10, 1940, 20808. PENNSYLVANIA: 1. Southeast of Mauch Chunk, July 10, 1940, 20809. 2. Northwest of Mauch Chunk, July 10, 1940, 20810. 3. Easton, July 14, 1940, 20811. 4. Ravine, July 11, 1940, 20812. 5. Ravine, July 11, 1940, 20813. 6. Muir, July 11, 1940, 20814. 7. Water Street, Sept. 18, 1939, 20815. 8. Along U. S. 30, Tuscarora Hill, July 11, 1940, 20816. 9. Along U. S. 30, Sideling Hill, July 11, 1940, 20817. 10. Laughlintown, Aug. 28, 1940, 20818. 11. Ten miles west of Erie, June 20, 1940, 20819. MARYLAND: 1. Rawlings, July 12, 1940, 20820. WEST VIRGINIA: 1. Romney, July 12, 1940, 20821. 2. Old Fields, July 12, 1940, 20822. 3. Franklin, July 12, 1940, 20823. INDIANA: 1. Jackson Co., about 2 miles east of Leesville, July, 1939, *R. M. Kreibel, C. F. McGraw & Morris Reeves*. 2. Back Creek, 1-1½ miles west of Leesville, July, 1940, *Kreibel, McGraw & Reeves*.

⁵ When a number is given without collector's name the writer was the collector.

⁶ A number not shown on maps 1 & 2 represents a station close to the preceding number.

OCURRENCE IN EACH COLLECTION OF THE FORMS OF *R. ODORATUS*

[illegible]

4. CORRELATION OF VARIATION WITH GEOGRAPHY

Cursory examination of table II shows but one fact, namely, that 4 of the forms occur essentially throughout the range of the species (as far as represented in these collections—see map 12), and 3 are more local. But from this list certain data may be derived; some of these data are shown on maps 1 and 2. Map 1 shows the percentage in each collection of individuals with leaves glabrous or glabrate beneath (or lacking glands above). For example, in collection 2 from Maine, a total of 25 individuals shows 4 f. *glabrifolius*, and 5 f. *heteradenius*, a total of 9 glabrous individuals, or 36 per cent—accordingly, the figure 36 appears next to the 2 in Maine. Similarly, collection 3 from New York has, in a total of 16 individuals, 1 f. *glabrifolius*, 8 f. *heteradenius*, and 3 *paraheteradenius*, making a total of 12 glabrous individuals, or 75 per cent—the figure appears near the 1 in New York, since collections 1–4 are too close together to be mapped separately.

How significant are the percentages shown on map 1? Probably not very significant individually, for the following reasons. First, the numbers in each collection are small, mostly below 50, sometimes less than 25. Second, *R. odoratus* spreads by underground stems, and more than one collection may be made from one individual (*i.e.*, clone). This has been avoided as far as possible by taking specimens at some distance from one another or from isolated plants.

When the figures from many collections are totaled, they become statistically more reliable. From Maine, 60 individuals have been collected, from Vermont 80, Massachusetts 29, Ontario 14, New York 448, Pennsylvania 256, Maryland 47, West Virginia 139, and Indiana 70. These represent many times the number of individuals ordinarily examined in the taxonomic treatment of a group, where a single sheet from a region is often taken to represent THE PLANT OF THAT REGION.

In determining the significance of figures from one patch of Flowering Raspberry, and the significance of those from a general region, the ecology of the species must be taken into consideration. Its favorite habitat is recently cut soil; it is

sometimes found on a river-cut bank, which may be more or less wooded, but its most frequent occurrence is along road-cuts. Nearly all of its stations are, therefore, more or less recent, the road-cuts being more recent than the river-cuts. But although any patch may be recent (and temporary) the species may be nevertheless of ancient occurrence in the region as a whole.

There is another important point regarding individual patches of *R. odoratus*—the seeds are, presumably, spread by birds, and the syncarp may contain seeds of different genetic constitutions (due to heterozygosity in the mother plant, and the possibility of pollen coming from several sources), and a colony may perhaps be started from a number of seeds dropped at one time; the variation within any patch should then be determined partly by the number of seeds originally dropped. If a colony increases in size vegetatively its original genetic constitution will tend to be preserved, while expansion by seeds will increase the number of forms. Again, the constitution of the species throughout a region stands as more significant than in any single patch.

With these facts in mind, map 1 may again be examined. It becomes evident that, in spite of lack of uniformity in many regions, the higher proportions of plants with glabrous leaves occur mostly toward the northern part of the range (omitting Indiana, for the present, as a more remote region). To emphasize this, we may divide the map into zones from north to south, by the broken lines running east and west. Within each of these zones the percentage of glabrous-leaved plants is determined (by totaling the figures from all the collections, not by averaging the percentages of each), with the result shown by the large figures along the right-hand margin of the map. There appears an unmistakable trend toward the appearance of velvety leaves southward and of glabrous leaves northward.⁷ With consideration of the line of farthest advance of

⁷ Perhaps it should be restated at this point that by "glabrous leaves" is meant also the glabrate or somewhat pilose leaves lacking glands on the upper surface, and by "velvety leaves" is meant those which tend to be more pubescent beneath and have dark glands above; cf. the key (page 303) and the discussion on page 301.

Pleistocene glaciation (line of crosses on map 10) a definite correlation appears. If it is assumed that *R. odoratus* survived glaciation south of the glaciated regions and migrated northward after the disappearance of the ice⁸ it becomes evident that the species became more glabrous as it spread northward. This has not involved the origin *en route* of a new character, for glabrous plants occur in the extreme southern part of the range (represented in the Gray Herbarium by sheets from Virginia, North Carolina, Kentucky and Tennessee) and velvety leaves occur in the extreme northern part of the range (specimens in the Gray Herbarium from Quebec and Nova Scotia), but rather a change in the proportion of occurrence of the character. Is this because (1) the glabrous plants are more suited, physiologically, to the northern regions, (2) the glabrous plants were for some reason more vigorous in spreading, or (3) simply that as the species migrated chance happened to favor partial elimination of pubescent individuals?

The situation regarding pubescence of leaves in *R. odoratus* is just the reverse of that regarding the pubescence of the stem in the Red Raspberry (*Rubus idaeus*, or *R. strigosus*). In the latter, the proportion of pubescent plants increases northward. Perhaps any purpose that may be ascribed to a hairy covering is of less effect than is the linkage of pubescence, or in other cases glabrousness, with other characters which have a closer relation to the environment.

Similar progressive variation has been demonstrated for the snail, *Partula suturalis*, in the isolated valleys on the island of Moorea.⁹ Eastward, colonies are composed entirely of dextral individuals, and these gradually give way, westward and northwestward, to colonies composed entirely of sinistral individuals (see map 11).

On map 2 are plotted the percentages of individuals in each colony with short glands on the pedicels (f. *bifarius* and f. *glabrifolius*). As on map 1, there is lack of uniformity from local-

⁸ This does not preclude the possibility of interglacial migration also.

⁹ Crampton, H. E. Studies on the variation, distribution, and evolution of the genus *Partula*: the species inhabiting Moorea. Carnegie Institution of Washington. Publ. 410. 1932.

ity to locality, but here, again, appear decided tendencies: the group of low figures in New York, for example, is striking. The series is not as definite from north to south as it was on map 1, but by grouping the localities as is shown by the broken lines on map 2 there can be demonstrated a fair uniformity within regions and great variation between regions. The tendency is not all in one direction as it was in pubescence of leaves. Starting with a low percentage (17) in the south, we find a rise as we go northeastward, a drop in the central region, and a sharp rise in the northern part. These facts favor the third hypothesis suggested above, namely, that as the species migrated there were slight changes in the frequencies of the characters due to chance or to unknown factors; with reference to pubescence of leaves all the changes were in the same direction, and with reference to the glands of the pedicels they were in different directions in different regions.

Two other characters appear in the key on page 303. One of these is the presence of sessile glands instead of definitely stalked glands on the pedicels. Only two individuals have been seen with this character, one from Chenango Bridge (New York no. 8) and the other from Sideling Hill (Pennsylvania no. 9). This small occurrence is of little significance except for comparison with the situation in *R. parviflorus*, where in the plant of the Great Lakes such sessile glands are found on only about 1 per cent of the plants (26 out of 2191 individuals collected), but in the western range of the species occur in much larger numbers (68 of 109 plants from the Black Hills of South Dakota, 98 of 242 plants from Montana, Wyoming and Utah, and 71 of 123 plants from Colorado). The remaining character used in the key lies in the stalked glands on the lower surface of the veins; ordinarily these do not exceed 1 mm., but on a majority of the plants from Indiana and from a very few elsewhere are hairs 1–2 mm. or more long. The occurrence of this character in large proportions only in the unglaciated part of Indiana is important, for it indicates a much more ancient migration from the Alleghenian center to Indiana than to New York and New England. Previous to the more recent glacia-

tions, at least, *R. odoratus* migrated westward, perhaps changing the frequency of some characters as it migrated. Either because of these changes or because of isolation as small populations¹⁰ in the southern Alleghenies and in Indiana the plants of these two regions became different: the eastern plants became predominantly velvety-leaved and those of Indiana entirely glabrous-leaved; in the East the presence of glands on the upper leaf-surfaces became generally associated with velvety lower surfaces while in Indiana they appeared freely associating with nearly glabrous lower surfaces; the eastern plants retained short glands on the pedicels in many cases while those of Indiana eliminated this character and retained only long glands; and, finally, the majority of plants of Indiana retained long glands on the veins of the lower leaf-surfaces, while only a small minority of eastern plants showed this character. Available material is insufficient for further study of this phase of migration and isolation (see map 12 for an indication of the proportion of the range of the species represented by mass collections), but collections from Virginia to Indiana and southward should yield interesting evidence.

It is now possible to combine data concerning all the characters discussed above, to discover closeness of relationship of plants in different regions. For this purpose, localities whose populations show the closest resemblance, all characters considered, have been grouped into regions. For example, collections 1-4 in New York, in the vicinity of Rochester (Station New York 1 on maps 1 & 2), agree in having a rather high percentage of glabrous leaves (86, 100, 75, 66, on map 1) and a rather low percentage of short-glanded pedicels (20, 0, 6, 33, on map 2). These four collections are thus treated as one regional unit, labelled "Rochester" on map 3. Localities 7 and 8 in Pennsylvania are in close agreement (both 0 for glabrous leaves, 42 and 64 respectively for short glands) and so are grouped together. The resulting regional groupings are shown on map 3, where each region is vertically shaded and labelled with a name. These regions appear to show little or no relation to physiographic features.

¹⁰ Compare Dobzhansky, *Genetics and the origin of species*, pp. 118-148. 1937.

The comparative values of figures from each region may be judged from the figure in parentheses just below each regional name on map 3, which indicates the number of individuals collected in that region. The numbers from Ontario and Mauch Chunk (Pennsylvania 1 and 2) are each only 14, so small that these regions are omitted from the map. On map 3 are also recorded the percentages for each of the four characters in which the plants vary, obtained by totaling and averaging for all the plants in each region; these percentages are combined into a pie-diagram for each region. For example, among the 60 plants from Maine there were 24 of f. *glabrifolius* and 11 of f. *heteradenius*, a total of 35 plants with leaves not velvety beneath, or 58 per cent; this is indicated on map 3 by a 58 placed in the upper quadrant of the pie-diagram for the Maine region. There were 24 f. *glabrifolius* and 12 f. *bifarius* to total 36 individuals with short glands on the pedicels, or 60 per cent; this is indicated by a 60 in the left quadrant in the pie-diagram. Subsessile glands on the pedicels, and long-stalked glands on the leaves below, are not represented in Maine, and this is indicated by zeros placed, respectively, in the lower and in the right quadrants.

In the pie-diagrams on map 3, figures of 100 or 0 indicate uniformity in the characters concerned, while figures approaching 50 indicate that the plants of the region are variable in the characters concerned.

From the figures on map 3 may be calculated the average of percentage differences between any two regions. To compare, for example, Maine with northern Vermont: velvety and glandular leaves *vs.* non-velvety and non-glandular leaves, shows a difference of 5 (63 per cent minus 58 per cent), long glands on the pedicels *vs.* short glands shows a difference of 44 (60 per cent minus 16 per cent), and there is no difference in the other two characters. The average of percentage differences (5 plus 44 plus zero plus zero, divided by 4) is 12. A comparison of Maine with Indiana, however, gives a much higher figure, adding 42 (100 minus 58), 60 (60 minus 0), 0 (0 minus 0), and 59 (59 minus 0), to average 40.

Table III shows in tabular form the averages of percentage

differences between all regions. From it may be made a number of correlations with the assumed post-glacial history of the species; these become more obvious when the data are transferred to maps.

TABLE III
AVERAGES OF DIFFERENCES OF PERCENTAGES BETWEEN REGIONS

	Maine	Northern Vermont	Rochester	Susquehanna	Western New York	Alleghany	Erie	Bear Mt.	Easton	Schuykill	Tuscarora	Potomac	Indiana
Maine	—	12	23	13	11	16	19	16	16	19	17	19	40
Northern Vermont	12	—	10	3	4	6	9	8	9	17	24	10	28
Rochester	23	10	—	11	13	15	18	17	7	28	35	19	18
Susquehanna	13	3	11	—	7	9	12	9	7	18	25	11	28
Western New York	11	4	13	7	—	3	7	8	13	19	26	11	27
Alleghany	16	6	15	9	3	—	9	10	15	20	27	12	25
Erie	19	9	18	12	7	9	—	3	18	13	20	4	33
Bear Mt.	16	8	17	9	8	10	3	—	15	11	18	3	34
Easton	16	9	7	7	13	15	18	15	—	21	28	18	25
Schuykill	19	17	28	18	19	20	13	11	21	—	7	9	45
Tuscarora	17	24	35	25	26	27	20	18	28	7	—	16	52
Potomac	19	10	19	11	11	12	4	3	18	9	16	—	37
Indiana	40	28	18	28	27	25	33	34	25	45	52	37	—

In general, regions which are close to each other show closer relationship than do regions more distant from each other; this is to be expected in a freely interbreeding population spread over a large area. But certain irregularities in this general pattern will appear in a species whose range has comparatively recently been altered by such an event as glaciation. This is brought out in map 4, which shows the close interrelationship of the regions across northwestern Pennsylvania, southern New York, and western New England (recently glaciated areas¹¹), fairly close interrelationship among the pre-Wisconsin regions from central Pennsylvania southward, but rather distant interrelationship between the pre-Wisconsin regions and the post-Wisconsin regions. This is brought out further in map 5 which shows only the more closely related regions.

¹¹ The Alleghany region was not actually glaciated, but was a tongue of unglaciated territory only 10 miles across and was probably untenable for *R. odoratus* during glaciation.

The Potomac region (map 6) and the Easton region (map 7) show relationship closer to most post-Wisconsin regions than to the much nearer pre-Wisconsin regions. This may be because the pre-Wisconsin stations have been isolated for a long time. Their close relationship with post-Wisconsin regions may indicate that much of the population of these regions was derived from the Potomac and the Easton regions. Furthermore, it seems to be more than a coincidence that in each general direction from the Potomac region, there is some correlation between geographic distance and distance of relationship—this is shown on map 6 by the sets of parallel lines emerging from the Potomac region. The Easton region is similar to the Potomac region in this respect.¹² The relation of each of these regions to other pre-Wisconsin regions is generally more remote than to the post-Wisconsin regions, and shows no correlation with geographic distance.

The relationships between the Tuscarora region and the other regions (map 8), and between the Schuylkill region and the other regions (map 9), show no correlation with distance. These regions are in general less closely related to the post-Wisconsin regions than are the Potomac region and the Easton region. Perhaps, then, there was greater contribution to the post-Wisconsin populations of the glaciated regions from the Potomac region and the Easton region than there was from Tuscarora region and the Schuylkill region. It must be borne in mind that other regions, not sampled in this study, might throw more light on this phase of the subject.

The relation of the Indiana region to all other regions is distant, and shows little or no correlation between geographic distance and relationship (map 10). This is compatible with the assumption that the isolation of *R. odoratus* in unglaciated southern Indiana greatly antedates the postglacial migration of that species into New York and New England.

It is conceivable that with full collections from every point in the range of the species, a map could be constructed along

¹² The Easton region was covered by the older ice sheets but not by the Wisconsin. Since the Easton region is represented in this study by a collection from but one locality, its figures are probably of less value than those from a region like Potomac with its six collections.

the lines of map 5, which would actually show the course of postglacial migration. How far map 5 falls short of representing the full facts may be judged from map 12, which shows the amount of coverage of the range of *R. odoratus* by the available mass collections.

II. VARIATION IN *R. parviflorus*

1. THE KINDS OF VARIATION

The more conspicuous variations within *R. parviflorus* are of the following ten types. On most of these characters, subdivisions of the species have, by one taxonomist or another, been proposed. To judge from the literature, no attempt has previously been made to assemble from each region a large amount of material for the purpose of determining just how many subdivisions of the species might grow together. This discussion is based primarily on 104 such collections totaling 2137 individuals; the proportion of the range thus covered may be judged by comparing map 24, which shows the known range of *R. parviflorus*, with map 19, showing the locations of mass collections. Material of the species in the Gray Herbarium, the New York Botanical Garden, the University of California, Pomona College, and the University of Wisconsin has also been studied.

1. Calyx villous or not villous. Individuals with villous calyces appear throughout a large part of the range of the species, always in company with a great majority of plants with the calyces not villous. Encountering villous calyces only in plants from the Great Lakes region in what he called var. *genuinus* and in var. *velutinus* from the Coast Ranges of California, Professor Fernald stated (*l. c.*, page 275) that these two varieties were closely related. When examined in the light of subsequent collections, which show villous calyces to occur throughout the range of the species, they seem to represent rather a sporadic variation, present in about a third of the plants from the Coast Ranges and a much smaller proportion of individuals from the rest of the range. In maps 20 and 21 the percentage of plants in each region with villous calyces is shown by the figure in the lowermost sector of each pie-diagram. Map 13 shows the occurrence of plants with villous calyces, except in California.

2. Glands or setae of the pedicels. These are of four types. (1) The glands may be on stalks about 0.5 mm. long. (2) The glands may be on stalks reaching 1–2 mm. in length, or rarely even longer. There seems to be no correlation of gland color with length of the stalk. (3) The glands may be sessile or on stalks less than one-fourth as long as the diameter of the gland, or rarely the glands may be entirely absent. (4) There may be, instead of glands, broad-based setae; this type is very rare, having been observed in only two collections. Types 1–3 occur practically throughout the range of the species, and in combination with any of the other characters. The occurrence of glands about 0.5 mm. long is shown on maps 13, 16, and 17; the occurrence of glands 1 mm. or more long is shown on maps 14 and 15; the occurrence of subsessile glands is shown on map 18. In addition to the ranges shown on these maps, types 1–3 also are found in the Coast Ranges of California. Types 1–3 are not always clear-cut, and may grade into each other.

3. Leaves velvety beneath or not velvety beneath. Lower leaf-surfaces grade from perfectly glabrous, through a condition where scattered appressed hairs are present, to densely velvety. Some of the intermediates make it difficult to maintain two categories. In the present study, those leaves which feel velvety to the touch are treated as such. Throughout most of the range of the species velvety leaves show little or no correlation with other characters; they are not common on plants with sessile glands on the pedicels, but such a combination occasionally occurs, particularly in California. In the Great Lakes region 1093 out of 1346 individuals examined had velvety leaves; in the Coast Ranges velvety leaves are the rule almost without exception, being present on all but one of the 327 individuals examined; in the intermediate region they are in the minority, occurring in 231 out of 660 plants examined. Maps 14 and 16 show the occurrence of velvety leaves, and maps 13, 15 and 17 show the occurrence of glabrous or subglabrous ones.

4. Petioles with minute puberulence beneath the glands, or without such puberulence. When studied in the Gray Herbarium by the writer, this character appeared to be of some importance, for, while common in the western states, puberulent petioles appeared only on one sheet from the Middle West, and this was from Keweenaw Point, Michigan, where a number of far western plants are known to occur. But examination of the mass collections made about the Great Lakes showed plants with puberulent petioles from throughout the entire range. Its complete lack of taxonomic value in this region is shown by the fact

that the leaves on the upper part of a stem may have puberulent petioles while the leaves farther down may have the petioles glabrous beneath the glands. It was just coincidence that the only sheet in the Gray Herbarium from the Middle West, showing puberulent petioles, was from Keweenaw Point. One thing about this character may be significant, however; while the puberulence of the petioles appears to be, for the most part, a response to exposure, nevertheless nearly all the plants from the Coast Ranges of California have all their petioles puberulent.

The exceptions are in a collection from Eureka (*Gillespie 15398*, described in tables v, vi & vii, pages 329, 332, 333), in which there is great variation. Most of the individuals have the stem and petioles copiously villous (character no. 6), as var. *velutinus*, some do not, and a few are intermediate. Some have the petioles puberulent and others do not. That this is not entirely due to habitat was demonstrated by growing the offspring of a few of these plants in the greenhouse at the University of Wisconsin. Plants grown from different seeds in one syncarp, under identical conditions in the greenhouse, showed the same variations that were present in the original collection.

5. Pedicels villous or not villous. Of the 248 individuals in the mass collections from the Coast Ranges of California, all but 42 are characterized by the presence of spreading hairs exceeding the glands on the pedicels. Of nearly 2000 individuals from the rest of the range of *R. parviflorus* only 3 have villous pedicels: two are from Wisconsin and one from southern California.

A collection from the District of Renfrew, Vancouver Island, *C. O. Rosendahl & Carl J. Brand, 3*, also has long hairs on the pedicels. This collection has been seen in the Herbarium of the University of California. The same collection, as it appears in the Herbarium of Pomona College, shows this characteristic to a lesser degree, and is probably from a different clone.

6. Stem, stipules and petioles villous or not villous. Plants of the Coast Ranges nearly always have these organs more or less villous (rarely sparsely so), and so are separated as var. *velutinus*, as distinguished from the rest of the species which lacks this character. For the correlation of this character with others see the discussion of var. *velutinus*, on page 318.

7. Cutting of leaves. *R. nutkanus* f. *lacera* Kuntze,¹³ or *R. parviflorus* var. *bifarius* f. *lacera* Fernald,¹⁴ has leaves cleft $\frac{2}{3}$ – $\frac{3}{4}$ to the base, and *R. parviflorus* f. *pedatifidus* Hermann¹⁵ has them cleft entirely to the base.

¹³ Meth. Sp. 102. 1879.

¹⁵ *Rhodora* 37: 61, pl. 326, fig. 2. 1935.

¹⁴ *Rhodora* 37: 281. 1935.

8. Cutting of sepals and petals. *R. parviflorus* var. *Fraserianus* J. K. Henry,¹⁶ or *R. parviflorus* var. *bifarius* f. *Fraserianus* Fernald,¹⁴ has the petals laciniate-dentate at summit, and a sheet from the Santa Cruz Mountains of California has the calyx-lobes laciniate.

9. Color of petals. The petals, white in most plants, are recorded on the labels as turning pink with age on sheets from Del Norte County, California, and from Mt. Hamilton, Washington.

10. Size of flowers. This varies considerably from clone to clone, but there seems to be no justification for the division into a larger-flowered western variety and smaller-flowered variety about the Great Lakes, such as has been proposed by Torrey & Gray¹⁷ and by Farwell.¹⁸ The smallest-flowered plants seen by the writer comprise a collection of 21 individuals from Tuolumne County, California (*Wiggins* 9245, described as California 1 in tables v and vi, pages 329 and 332); the flowers are about 2.5 cm. in diameter, with a calyx sometimes as little as 12 mm. in diameter. This small-flowered extreme may be identified, by the latest taxonomic treatment of the *R. parviflorus* group,¹⁹ as "var. *grandiflorus*."

It is evident that here are variations of several series. Groups 7, 8, 9 and 10 include sporadic anomalies of rare occurrence, apparently occurring anywhere throughout the range of the species without relation to each other or to the other series of variations. Groups 1-6 are concerned with pubescence. Groups 1, 2 and 3 have been used by Professor Fernald to distinguish varieties; an appraisal of these varieties in the light of new and more ample material follows.

2. THE "VARIETIES" OF *R. parviflorus*

1. *R. parviflorus* var. *genuinus* Fernald, *Rhodora* 37: 277. 1935. This is distinguished by its villous calyx and is said to be confined to the region of the upper Great Lakes; the present writer has collected it from a much wider range (map 13). The case against var. *genuinus*, as defined by Fernald, lies in the fact that its main character, a villous calyx, may appear anywhere throughout the range of the species, in various combinations with other characters, for plants with villous calyx may have pedicels with long glands (like vars. *hypomalacus* and *heteradenius*), or short glands (like vars. *bifarius* and *grandiflorus*), or sessile glands (like vars. *scopulorum* and *parvifolius*); the leaves may be glabrous or glabrate beneath (like vars. *heteradenius* and *grandiflorus*) or soft-pubescent (like vars. *hypomalacus* and *bifarius*).

¹⁶ *Torrey* 18: 54, fig. 1. 1918.

¹⁸ *Am. Midl. Nat.* 11: 281. 1929.

¹⁷ *Fl. N. Am.* 1: 450. 1840.

¹⁹ *Rhodora* 37: 276. 1935.

2. *R. parviflorus* var. *velutinus* (Hook. & Arn.) Greene, as defined by Fernald, *l. c.*, is distinguished from vars. *hypomalacus* and *bifarius* only by its villous calyx. But all individuals of these so-called varieties, as they occur in the Coast Ranges (to which region, as Fernald correctly states, var. *velutinus* is confined), are characterized by having long spreading hairs on the nodal regions, often the internodes, and the petioles, and by strigose stipules; these characteristics do not occur elsewhere in the range of *R. parviflorus*. In other words, the plants of the Coast Ranges may or may not have the calyx villous and may have the glands of the pedicels long or short, but they are set off from the rest of the species by the pubescence of the nodes, petioles and stipules. Var. *velutinus*, as redefined on the basis of this character, also differs in tendencies from the rest of the species as follows: in var. *velutinus* 83 per cent of the individuals in the mass collections have long hairs on the pedicels, 33 per cent have villous calyces, and 100 per cent have leaves velvety beneath, whereas in the rest of the range of *R. parviflorus* only 0.0015 per cent of the individuals have long hairs on the pedicels, 0.019 per cent have villous calyces, and about 64 per cent have leaves velvety beneath. These facts are brought out visually in map 20, where the pattern of the pie-diagram for the Coast Ranges is conspicuously different from all the others. Var. *velutinus* is therefore retained as a valid geographic variety, but on different characters, in part, from those relied on by Professor Fernald.

3. *R. parviflorus* var. *hypomalacus* Fernald, *l. c.*, p. 277, (4) var. *heteradenius* Fernald, *l. c.*, p. 279, (5) var. *bifarius* Fernald, *l. c.*, p. 280, and (6) var. *grandiflorus* Farwell, as redefined by Fernald, *l. c.*, p. 281. The 2 characters of long glands *vs.* short glands on the pedicels, and leaves velvety beneath *vs.* leaves glabrous to glabrate beneath, occur in 4 combinations to make these 4 varieties. Their ranges as published by Professor Fernald (dots on maps 14-17 in this paper) are rather similar, the only significant departure from the general pattern being that var. *grandiflorus* alone occurs in South Dakota, southern Montana, Wyoming, Utah and Idaho. Even this amount of geographic segregation seems to break down with other collections, as shown by the x's on these same maps. Moreover there is very little segregation of these "varieties" in the field. Of 8 mass collections from Minnesota, 2 collections had 4 of these "varieties," 2 had 3 "varieties," 3 had 2 "varieties," and 1 had 1 "variety." This statement refers only to the 4 "varieties" whose names head this paragraph; in many cases others were also present. Of 6 mass collections from northern Wisconsin, 1 had 4 "varieties," 3 had 3 "varieties," 1 had 2 "varieties,"

and 1 had 1 "variety." Such cases might be cited indefinitely, but the mass collections are described in tables VI & VII.

As stated in the discussion of that variety, the var. *genuinus* of Fernald breaks up on just the characters used by him to define vars. *hypomalacus*, *heteradenius*, *bifarius* and *grandiflorus*. Var. *velutinus*, as defined by Fernald, has subdivisions equivalent to vars. *hypomalacus* and *bifarius*. Var. *scopulorum* has a phase with velvety leaves and a phase with glabrous or glabrate leaves.

It is concluded, then, that in the absence of segregation of vars. *hypomalacus*, *heteradenius*, *bifarius* and *grandiflorus* on basis of geographic distribution, habitat, or locality, they represent forms only.

7. *R. parviflorus* var. *scopulorum* (Greene) Fernald, and (8) var. *parvifolius* (Gray) Fernald. These are distinguished from each other by the height of the plant, the width and pubescence of the leaves, the number of flowers in the inflorescence, and the length of the lowest pedicel. These distinctions do not hold in the field. Two collections in the gorge of Fish Creek Falls, Steamboat Springs, Colorado (pl. 10, fig. 4), consisted of some plants with sessile glands and others with stalked glands on the pedicels. The characters of those with sessile glands may be seen, in table IV, to make very difficult any separation into two groups such as have been named *scopulorum* and *parvifolius*.

These two so-called varieties with glands of the pedicel sessile or nearly so are recorded by Professor Fernald as occurring only from southern British Columbia, Oregon and Montana, southward to Arizona, New Mexico and northern Chihuahua. However, there are, in the herbaria of the University of California and of Pomona College, numerous specimens from California having the glands of the pedicels sessile or nearly so; they have leaves velvety beneath and cannot be placed by Fernald's key. The present writer has collected plants with sessile glands (always accompanied by others with stalked glands) in the Black Hills of South Dakota and in the three Great Lakes states where *R. parviflorus* is known. Map 18 shows the occurrence of plants with sessile or subsessile glands, as originally mapped by Fernald, and as demonstrated by other collections not seen by him.

The sessile or subsessile gland is not clear-cut from the stipitate gland; a distinction between them forms the primary division in Professor Fernald's key. Var. *scopulorum* (including var. *parvifolius*) with glabrous leaves grades into var. *grandiflorus*, and its unnamed relative with pubescent leaves grades into var. *bifarius*.

The case against vars. *scopulorum* and *parvifolius*, then, sums up as follows: the two are not distinct from each other in the field; they

TABLE IV
CHARACTERS OF VAR. *SCOPULORUM* AND VAR. *PARVIFOLIUS*, AND OF
TWO MASS COLLECTIONS FROM FISH CREEK FALLS,
STEAMBOAT SPRINGS, COLORADO

	<i>scopulorum</i>	<i>parvifolius</i>	Fish Creek Falls I	Fish Creek Falls II
Height of plant	1-2 m.	1.5-6.0 dm.	0.4-1.5 m.	
Width of leaves	1-3 dm.	0.5-1.3 dm.	1.2-2.4 dm.	1.0-1.9 dm.
Lower surface of leaves	Glabrous	Minutely and sparsely pubescent to glabrate	Glabrous to distinctly velvety	Glabrous to distinctly velvety
Number of flowers in inflorescence	3-7	1-2 (-4)	2 with 2 fl. 8 with 3 fl. 4 with 4 fl. 1 with 5 fl.	4 with 1 fl. 5 with 2 fl. 7 with 3 fl. 3 with 4 fl.
Length of lowest peduncle	1.0-3.5 cm.	2.0-6.0 cm.	1.5 cm. on 1 2.0 cm. on 3 2.5 cm. on 3 3.0 cm. on 2 3.5 cm. on 2 4.0 cm. on 6 4.5 cm. on 1 5.5 cm. on 1 6.0 cm. on 1	1.0 cm. on 1 2.0 cm. on 6 2.5 cm. on 1 3.0 cm. on 5 3.5 cm. on 3 4.0 cm. on 1 5.0 cm. on 1 6.0 cm. on 1

occur with and grade into vars. *grandiflorus* and *bifarius*; the sessile gland is not correlated with a glabrous or glabrate leaf; they are not confined to any limited part of the range of the species, but may rather be found in the same patch with the other "varieties" almost (or perhaps quite) everywhere that *R. parviflorus* grows.

Mr. Joseph Ewan, of the University of Colorado, who has kindly read the manuscript of this paper, comments as follows on the disposition of var. *parvifolius*:

"In my opinion there is something valid about the thing isolated by Fernald, following earlier segregations, centering about New Mexico and Arizona. I have personally discovered, without any particular search in herbaria for them, several 'good' sheets of that entity. It is characterized by the concomitance of definitely smaller leaves than any other variety or subspecies of the species, with fewer flowers to an inflorescence, and a slender habit. I do not feel that *scopulorum* is more than a form, of indefinite lines at best, but this southern phase of the species deserves, I believe, recognition. . . . Your collection from Fish Creek Falls, Steamboat Springs, Colorado, illustrates a representative of the zone of overlap between var. *parvifolius* and f. *scopulorum*, if such a form is to be recognized, even demonstrating perhaps a hybrid swarm dating from a long time ago in the movements of this *Rubus*."

These comments are introduced so that botanists in the Southwest may have opportunity to observe and perhaps decide upon the validity of this small-leaved phase of the species. For the present, var. *parvifolius* is put into synonymy under f. *scopulorum* (page 323), and its revival would cause no nomenclatorial complication and require no new combination.

Here, then, is a set of characters appearing in different combinations, with any combination of characters being likely to occur anywhere in the range of the species. Such combinations of characters, lacking geographic ranges, are not usually treated as varieties, but as forms, if they indeed receive any nomenclatorial recognition.

Professor Fernald emphasizes²⁰ the “disconcerting but indisputable fact that these very differences in the distribution of glands in the inflorescence and of pilosity on the calices, branches and leaves or the absence of glands and pilosity from these areas, which mark the eight geographic segregates of *Rubus parviflorus*, are precisely the characters which are shuffled and reshuffled to add to the ever increasing score of ‘species’ of Blackberry (*Rubus* § *Eubatus*)! In *R. parviflorus* not even our most ardent advocates of specific segregation, who have felt competent to make generic segregates, have noticed them; nevertheless, they are quite as conspicuous in *R. parviflorus* as in segregates of *Rubus* § *Eubatus*, and if their phylogenetic importance is of equal value in the two sections, the Blackberries are eventually due for a pretty drastic realignment.” The “if” in the last statement was commented upon by Professor Fernald, a few years ago,²¹ in these very pertinent words: “As pure logic, wholly dissociated from the actual vagaries of Nature, this may be conceded; but, surely, when applied in classification, the logic often fails; characters which in one group are of great taxonomic importance in another may prove wholly unimportant and to be a series of nonconcomitant and unresolvable variables.”

The taxonomic value of characters lies less in what they do in other groups, or in how conspicuous they may be, than in how they act. Pubescence of stem and peduncles is used as a

²⁰ Rhodora 37: 274. 1935.

²¹ Rhodora 35: 165. 1933.

primary character in separating species of *Stellaria*,²² is of varietal rank in *Ranunculus abortivus*,²³ and serves only to separate forms in *Oxalis europaea*.²⁴ Again in *O. europaea*, while differences in pubescence of stem and pedicels are used only to separate forms, the presence or absence of scattered hairs on the upper surface of leaflets differentiates varieties; this is not because pubescence of leaflet surface is more conspicuous or perhaps of greater importance to the plant, but because plants with such pubescence are found in different regions from those which lack it. This principle is summarized by Anderson²⁵ when he writes: "Particularly significant is the fact that the difference between *I. virginica* and *I. virginica* var. *Shrevei* is of about the same order of magnitude as the differences between colonies of *I. virginica* var. *Shrevei*. It would indeed be possible to find two swamps in the same township in southern Michigan whose iris populations have as great an average difference as that between *Iris virginica* of the Atlantic Coastal plain and *Iris virginica* var. *Shrevei*. But in this latter case the difference, slight though it is, characterizes a whole region and has superimposed upon it the varying pattern of colony differences in each region."

Summary: With the exception of var. *velutinus*, the varieties of *Rubus parviflorus* described by Professor Fernald appear invalid to the present writer, for the following reasons. (1) The entities are not confined to the ranges described by him, but each occurs nearly throughout the range of the species. (2) Rare is the colony that is composed of but one entity, and many colonies are composed of a mixture of as many as five entities. (3) There seems to be little or no association of characters one with another, since they may appear in almost any combination, many of these combinations being impossible to place in Fernald's key to varieties.

3. THE FORMS OF *R. parviflorus*

The advisability of giving a formal name to each recombination of certain pubescence characters may be debatable, and

²² Gray's Man., ed. 7, p. 381. 1908.

²³ Fernald, Rhodora 40: 417. 1938.

²⁴ Wiegand, Rhodora 27: 135. 1925.

²⁵ Ann. Mo. Bot. Gard. 23: 494. 1936.

a list of nearly a score of new names within one species is apt to make the taxonomist gasp.²⁶ The present writer is of the opinion that forms should be named if the naming of them will serve a purpose. A group is named so that "we may be understood when we wish to speak of it."²⁷ There is to be occasion to speak of these combinations of characters, to discuss the significance of the occurrence of each, and eventually to distribute material illustrative of them, and these procedures will be facilitated by the assignment of names to them.

The following were treated as varieties by Professor Fernald:

R. PARVIFLORUS f. **hypomalacus** (Fernald) n. comb. *R. parviflorus* var. *hypomalacus* Fernald, *Rhodora* **37**: 277. 1935.

R. PARVIFLORUS f. **heteradenius** (Fernald) n. comb. *R. parviflorus* var. *heteradenius* Fernald, *l. c.*, 279.

R. PARVIFLORUS f. **bifarius** (Fernald) n. comb. *R. parviflorus* var. *bifarius* Fernald, *l. c.*, 280.

R. PARVIFLORUS f. **glabrifolius**, n.f., foliis subtus glabris vel glabratiss vel sparse appresso-pilosis; pedicellorum glandulis stipitatis 0.5–1.0 mm. longis; calycibus non villosis.—TYPE, in Herb. Univ. Wis.: small patch along roadside, 3.6 miles west of Meldrum Bay, Ontario, Aug. 5, 1939, *Fassett* 20567. *R. parviflorus* var. *grandiflorus* Fernald, *l. c.*, 281; perhaps *R. parviflorus* var. *grandiflora* Farwell, *Am. Midl. Nat.* **11**: 263. 1929.

R. PARVIFLORUS f. **scopulorum** (Greene) n. comb. *R. nutkanus* var. *scopulorum* Greene ex Focke, *Bibl. Bot.* **17**, pt. 72: 124. 1911. *R. parviflorus* var. *scopulorum* Fernald, *l. c.*, 283. *R. nutkanus* var. *parvifolius* Gray, *Pl. Fendl.*, *Mem. Am. Acad.* **II**, **4**: 42. 1849. *R. parviflorus* var. *parvifolius* Fernald, *l. c.*, 284. In uniting these two varieties as one form, it seems advisable to use the name *scopulorum* rather than the one antedating it (in the varietal rank), which not only emphasizes a character not necessarily applicable to the plant but whose resemblance to the specific name is liable to invite confusion.

R. PARVIFLORUS f. **Nuttallii** (Torr. & Gr.) n. comb. *R. parviflorus* Nutt., *Gen.* **1**: 308. 1818. *R. nutkanus* β *Nuttallii* Torr. & Gr., *Fl. N.*

²⁶ "If one were to attempt to name *formae* in *Rubus* the result might be appalling. One may note minor variations but there is no necessity to give them Latin names or to restrict them to formal categories." L. H. Bailey, *Gentes Herbarum* **5**, Fasc. I. 19. 1941.

²⁷ The Vienna Rules of Nomenclature. *Rhodora* **9**: 36. 1907.

Am. 1: 450. 1840. *R. parviflorus* var. *genuinus* Fernald, *l. c.*, 277. The phrase in Nuttall's description, "segments of the calix villous," would seem to indicate the plant treated by Professor Fernald as var. *genuinus*, but the Nuttall specimen from Michilimackinac Island is the plant called by Fernald var. *grandiflorus*, and in this treatment f. *glabrifolius*. The name on the label is not preceded by an asterisk so its position as type is not secure, and the label bears the note "lost all but this fragment." Perhaps the villous calyx was observed by Nuttall on material subsequently lost. On the sheet with the Nuttall specimen are three others: one was collected by R. H. Kern in New Mexico; the second by Dr. Tiling in Sitka; and the third, without label, is definitely the var. *velutinus* of the Coast Ranges, having strongly villous calyces, and is mounted so that it partly overlies and partly underlies the Nuttall plant. Less confusion will be caused by following Nuttall's description, as Professor Fernald did, than by trying to redistribute names on the basis of this sheet.

The following forms are the results of other combinations of the characters used in the determination of varieties by Professor Fernald:

R. PARVIFLORUS f. **trichophorus**, n.f., f. *bifarium* simulans sed calycibus villosis. TYPE, in Herb. Univ. Wis.: Bark Point, Bayfield Co., Wis., July 10, 1938, *N. C. Fassett & J. T. Curtis 20545*.

R. PARVIFLORUS f. **villosus**, n.f., f. *hypomalacum* simulans sed calycibus villosis. TYPE, in Herb. Univ. Wis.: near head of Nigger Grade, Palomar Mt., San Diego Co., Calif., Aug. 4, 1938, *Frank F. Gander 6239*.

R. PARVIFLORUS f. **allocalyx**, n.f., f. *scopulorum* simulans, sed calycibus villosis. TYPE, in Herb. Univ. Wis.: 7 miles north of Savoy, S. D., June 26, 1939, *Fassett 20201*.

R. PARVIFLORUS f. **micradenius**, n.f., f. *scopulorum* simulans, sed foliis subtus velutinus. TYPE, in Herb. Univ. Wis.: gorge below Fish Creek Falls, Steamboat Springs, Colo., July 3, 1939, *Fassett 20193*.

A rare type of epidermal outgrowth on the pedicels, not accounted for in Professor Fernald's treatment, is a glandless flattened trichome 0.5–1.0 mm. long. This is associated with glabrous leaves in one case, and with velvety leaves in another.

R. PARVIFLORUS f. **adenius**, n.f., pedicellorum setis 0.5–1.0 mm. longis eglandulosis; foliis subtus subglabratiss. TYPE, in Herb. Univ. Wis.: sand back of dunes, Whitefish Bay, Door Co., Wis., July 31, 1938, *Fassett 20211*.

R. PARVIFLORUS f. **acephalus**, n.f., f. *adenium* simulans sed foliis subtus subvelutinis. TYPE, in Herb. Univ. Wis.: Port Orford, Ore., Aug. 12, 1938, *Doris K. Gillespie* 15399.

R. parviflorus var. *velutinus*, confined to the Coast Ranges of California, shows variations just paralleling those in the rest of the species. In studying the fluctuations of var. *velutinus* the writer has had the advantage of the loan of the material from the herbaria of the University of California and of Pomona College, as well as the most generous mass collections made by Drs. Gillespie, Mathias, Schreiber, Constance and Wiggins. To keep clear the parallelism of forms, each one in var. *velutinus* is here given a name based on that of the corresponding form in the widespread phase of the species.

R. PARVIFLORUS var. VELUTINUS f. **parbifarius**, n.f., caulibus, petiolis, pedicellis pedunculisque villosis; foliis subtus velutinis; pedicellorum glandulis stipitatis 0.5–1.0 mm. longis. TYPE, in Herb. Univ. Wis.: north slope of Strawberry Creek Canyon, 0.7 miles above its mouth, 1100 ft. alt., Berkeley, Calif., Aug. 4, 1938, *L. Constance* 2397.

R. PARVIFLORUS var. VELUTINUS f. **praebifarius**, n.f., f. *parbifarium* simulans sed pedicellis non villosis. TYPE, in Herb. Univ. Wis.: Eureka, Calif., Aug. 6, 1938, *Doris K. Gillespie* 15397.

R. PARVIFLORUS var. VELUTINUS f. **paratrichophorus**, n.f., f. *parbifarium* simulans sed calycibus villosis. TYPE, in Herb. Univ. Wis.: under *Sequoia sempervirens*, $\frac{1}{2}$ –1 mile from the ocean, Palo Colorado Canyon, Santa Lucia Mts., about 12 miles south of Carmel, Calif., Aug. 7, 1938, *Mildred E. Mathias* 1389.

R. PARVIFLORUS var. VELUTINUS f. **parahypomalacus**, n.f., caulibus, petiolis, pedicellis, pedunculisque villosis; calycibus non villosis vel subvillosis ad basem; pedicellorum pedunculorumque glandulis stipitatis 1–2 mm. longis. TYPE, in Herb. Univ. Wis.: 1.5 miles southeast of Abbot's Lagoon, Marin Co., Calif., Aug. 6, 1938, *Beryl O. Schreiber* 2538.

R. PARVIFLORUS var. VELUTINUS f. **isohypomalacus**, n.f., nodis stipulisque villosis; pedicellis calycibusque non villosis; pedicellorum pedunculorumque glandulis stipitatis 1.0–1.5 mm. longis. TYPE, in Herb. Univ. Wis.: Elk River 6 miles south of Eureka, Calif., Aug. 8, 1938, *Doris K. Gillespie* 15398.

R. PARVIFLORUS var. VELUTINUS f. **parvillosus**, n.f., caulibus, petiolis, pedunculis, pedicellis, calycibusque villosis; pedicellorum pedunculorumque glandulis stipitatis 1–2 mm. longis. TYPE, in Herb. Univ.

Wis.: 1.5 miles southeast of Abbot's Lagoon, Marin Co., Calif., Aug. 6, 1938, *Beryl O. Schreiber* 2538.

R. PARVIFLORUS var. *VELUTINUS* f. ***paramicradenius***, n.f., caulibus stipulisque sparse villosis; pedicellorum pedunculorumque glandulis subsessilibus. TYPE, in Herb. Univ. Wis.: Eureka, Calif., Aug. 6, 1938, *Doris K. Gillespie* 15397.

KEY TO VARIETIES AND FORMS OF *R. PARVIFLORUS*

- a. Stem, stipules and petioles without long spreading hairs; leaves of thin texture, not rugose above, their lower surfaces glabrous, glabrate, appressed-pubescent, or moderately velvety; pedicels only very exceptionally with long hairs exceeding the glands; petioles with or without a minute puberulence much shorter than the glands.....var. *genuinus*
- b. Pedicels with setae which are usually gland-tipped, the stalks more than 4 times as long as the diameter of the gland
- c. Setae of the pedicels gland-tipped
- d. Setae 1-2 mm. long
 - a. Leaves soft-pubescent beneath
 - f. Calyx not villous.....f. *hypomalacus*
 - f. Calyx with villous hairs hiding the glands.....f. *villosus*
 - e. Leaves not soft-pubescent beneath.....f. *heteradenius*
- d. Setae mostly about 0.5 mm. long
 - g. Leaves soft-pubescent beneath
 - h. Calyx not villous.....f. *bifarius*
 - h. Calyx with villous hairs hiding the glands.....f. *trichophorus*
 - g. Leaves not soft-pubescent beneath
 - i. Calyx not villous.....f. *glabrifolius*
 - i. Calyx with villous hairs hiding the glands.....f. *Nuttallii*
- e. Setae broad-based and not gland-tipped
 - j. Leaves soft-pubescent beneath.....f. *acephalus*
 - j. Leaves not soft-pubescent beneath.....f. *adenius*
- b. Pedicels glandless or with sessile glands or with glands on stalks less than 4 times as long as the diameter of the gland
 - k. Leaves soft-pubescent beneath.....f. *micradenius*
 - k. Leaves not soft-pubescent beneath
 - l. Calyx not villous.....f. *scopulorum*
 - l. Calyx with villous hairs hiding the glands.....f. *allocalyx*
- a. Stem, stipules and petioles with long spreading hairs; leaves of thickish texture, rugose above, their lower surfaces always densely velvety; pedicels usually with long hairs exceeding the glands; petioles always with a minute puberulence much shorter than the glands.....var. *velutinus*
- m. Pedicels with copious villous hairs exceeding the glands
 - n. Gland-tipped setae of pedicels 1-2 mm. long
 - o. Calyx not villous.....var. *velutinus* f. *parahypomalacus*
 - o. Calyx with villous hairs hiding the glands....var. *velutinus* f. *parvillosus*
 - n. Gland-tipped setae of pedicels about 0.5 mm. long
 - p. Calyx not villous.....var. *velutinus* f. *parbifarius*

- p.* Calyx with villous hairs hiding the glands.....
.....var. *velutinus* f. *paratrichophorus*
- m.* Pedicels without villous hairs exceeding the glands
- q.* Glands of pedicels on stalks 0.5 mm. or more long
 - r.* Glands of pedicels on stalks 0.5–1.0 mm. long.....
.....var. *velutinus* f. *praebifarius*
 - r.* Glands of pedicels on stalks 1.0–1.5 mm. long.....
.....var. *velutinus* f. *isohypomalacus*
 - q.* Glands of pedicels sessile or nearly so....var. *velutinus* f. *paramicradenius*

4. OCCURRENCE OF FORMS IN MASS COLLECTIONS

Table v is a list of localities where mass collections have been made. Each is numbered, and the numbers refer to localities shown by slanted figures on map 19. Table vi lists the number of individuals of each form represented in each collection.

TABLE V

ONTARIO: 1. Scattered in woods along the road to Cameron Lake, 6 miles south of Tobemory, Aug. 3, 1938, 20563. 2. Small patch in clearing, 8 miles east of Meldrum Bay, Aug. 4, 1939, 20566. 3. Large patch along the road and a few in the woods, 7.2 miles east of Meldrum Bay, Aug. 4, 1939, 20565. 4. Small patch along the road, 1.7 miles east of Meldrum Bay, Aug. 4, 1939, 20567. 5. Roadsides and openings in woods, 1 mile southwest of Meldrum Bay, Aug. 5, 1939, 20568. 6. Small patch along roadside, 3.6 miles west of Meldrum Bay, Aug. 5, 1939, 20569. 7. Widely scattered patches in spruce-fir and alder woods, 0.7 miles west of Meldrum Bay, Aug. 5, 1939, 20570. 8. Scattered in woods and on raised beach, a little along roadside, Meldrum Bay, Aug. 5, 1939, 20571. 9. Thicket and openings near Sterling Bay, southern tip of St. Joseph Island, Aug. 3, 1939, 20564. MICHIGAN: 1. In birch woods on raised cobblestone (limestone) beach, Gross Cap, 7 miles northwest of St. Ignace, Aug. 1, 1938, 20602. 2. Woods at the head of a sand beach, Pointe aux Barques, Aug. 1, 1938, 20601. 3. Roadside and pastured woods (aspen, birch, white cedar) 2 miles southwest of Garden City, Aug. 1, 1938, 20600. 4. Widespread along roadside and in woods (white cedar, white spruce, birch), Fairport, Aug. 1, 1938, 20603. 5. Roadside and along path in woods (fir, white spruce, birch), 5 miles south of Ford River, July 31, 1938, 20580. 6. Abundant along the abandoned highway and rare along relocated highway, north of Cedar River, Aug. 1, 1938, 20604. 7. Sparse among bracken in aspen woods, 6 miles north of Faithorn, July 30, 1938, 20598. 8. Small patch in aspen and Norway pine, 1 mile north of Faithorn, July 30, 1938, 20599. 9. Scattered, woods and talus of West Bluff, Keweenaw Peninsula, July 29, 1938, 20494. 10. Scattered in fir-white cedar woods near Lake Upson, Keweenaw Peninsula, July 29, 1938, 20557. 11. Abundant along roadside, 4 miles southwest of Eagle Harbor, July 29, 1938, 20558. 12. Woods and roadsides east of Mohawk, July 29, 1938, 20556. 13. Scattered in woods at summit of Wheel Kate, South Range, July 29, 1938, 20561. 14. Pathway up Wheel Kate, July 29, 1938, 20577. 15. Roadside 2 miles east of Painesdale, July 29, 1938, 20560. 16. Woods and roadsides, Toivola, July 29, 1938, 20495. 17. Big Limestone Mountain, near

L'Anse, July 29, 1938, 20493. 18. Old embankment (highway or R.R.?), Lake Mine, July 29, 1938, 20578. 19. Road fill 2 miles southeast of Ontonagon, July 29, 1938, 20574. 20. Mouth of Iron River west of Ontonagon, July 29, 1938, 20562. 21. Near Ontonagon River, June 28, 1939, *J. T. Curtis*. 22. Woods and sunny bank, Michigamme, July 30, 1938, 20576. 23. Pathway to Carp Lake Mine, Porcupine Mts., July 29, 1938, 20573. 24. Foot of talus below Carp Lake Mine, Porcupine Mts., July 29, 1938, 20555. 25. Same, one clone, 20559. 26. Woods and roadside west of Carp Lake Mine, Porcupine Mts., July 29, 1938, 20579. 27. Woods and roadsides, south end of Lake Gogebic, July 28, 1938, 20575. WISCONSIN: 1. Scattered along edge of woods, Lake Michigan shore, North Landing, at northern tip of Door Co., July 31, 1938, 20513. 2. Roadside, North Landing, July 31, 1938, 20514. 3. Almost solid along Lake Michigan shore, Rowleys Bay, July 31, 1938, 20508. 4. Roadside and woods (beech and white pine), North Bay, July 31, 1938, 20526. 5. Among white pine, hemlock, mountain maple, Baileys Harbor, Aug. 5, 1938, *Chester Cook*, C92. 6. Woods and clearing near Kangaroo Lake, Baileys Harbor, July 31, 1938, 20515. 7. Heavy woods along roadside, Jacksonport, July 20, 1938, *E. M. Gilbert & N. C. Fassett* 20509. 8. Same data, 20510. 9. Abundant in sand back of dunes, among oak, white pine, hemlock, birch and poison ivy, Whitefish Bay, July 31, 1938, 20211. 10. Road through woods, Lily Bay, July 31, 1938, 20529. 11. Gills Rock, July 31, 1938, 20530. 12. Scattered along roadside among beech, birch, white cedar, Sister Bay, July 31, 1938, 20527. 13. Field and roadside, Peninsula State Park, near Fish Creek, July 31, 1938, 20511. 14. Peninsula State Park, July 22, 1939, 20512. 15. Wooded bank near Wilcat Lake, north of Boulder Junction, July 28, 1938, 20543. 16. Jute Lake fire tower, northeast of Boulder Junction, July 5, 1939, *J. T. Curtis*. 17. Barksdale, July 8, 1938, 20541. 18. Woods and pathways, Oak Island, off Bayfield Co., July 9, 1938, *N. C. Fassett, J. T. Curtis & Louis Knowlton* 20544. 19. Roadside and red clay gully, Bark Point, July 10, 1938, *Fassett & Curtis* 20545. 20. Steep banks below Manitou Falls, Pattison State Park, July 14, 1938, 20542. MINNESOTA: 1. Apparently adventive, roadside 4 miles southeast of Gull Lake, Gunflint Trail north of Grand Marais, July 12, 1938, *Fassett & Curtis* 20538. 2. Near Loon Lake, 10.8 miles south of Gull Lake, July 12, 1938, *Fassett & Curtis* 20533. 3. Woods and roadside 13.7 miles south of Gull Lake, July 12, 1938, *Fassett & Curtis* 20532. 4. Roadsides and beaches of Lake Superior near mouth of Kadunce River 8 miles east of Grand Marais, July 12, 1938, *Fassett & Curtis* 20537. 5. Abundant in old logging road 1.5 miles from shore, Lutsen, July 13, 1938, *Fassett & Curtis* 20531. 6. Manitou Falls, July 13, 1938, *Fassett & Curtis* 20534. 7. Illgen City, July 13, 1938, *Fassett & Curtis* 20535. 8. Gooseberry River, July 13, 1938, *Fassett & Curtis* 20536. SOUTH DAKOTA: 1. Shady places in canyon south of Pluma, June 26, 1939, 20199. 2. Hillside near Pluma, June 26, 1939, 20200. 3. North-facing bluff, Fantail, near Lead, June 26, 1939, 20864. 4. Frequent in damp pine woods at alt. 2500 ft., Terry, July 2, 1939, *H. C. Cutler* 2622. 5. Woods 3 miles south of Savoy, June 26, 1939, 20198. 6. Open ground, 7 miles north of Savoy, June 26, 1939, 20201. ALBERTA: 1. Bordering an aspen grove, near Beaver Mines, about 12 miles west of Pincher Creek, foothills region, southeast of Crow's Nest Pass, June 30, 1940, *E. H. Moss*. 2. Under aspen and spruce, 10 miles west of Pincher Creek, July 1, 1940, *Moss*. 3. In lodgepole pine woods near Waterton, Waterton Lakes Park, June 29, 1940, *Moss*. 4. Edge of woods

and close to shore, same region and date, *Moss*. MONTANA: 1. North slope, alt. 5500 ft., Bear Canyon east of Bozeman, Aug. 11, 1938, *F. B. Cotner*. WYOMING: 1. Sunny bank near Steamboat Point, Yellowstone National Park,²⁸ June 28, 1939, 20209. 2. Near Sylvan Pass, Yellowstone National Park, June 28, 1939, 20205. 3. Near Tower Falls Junction, Yellowstone National Park, June 28, 1939, 20208. 4. Thicket on east side of Jenny Lake, Grand Teton National Park, June 29, 1939, 20206. 5. Camp ground in Hoback Canyon, June 29, 1939, 20207. UTAH: 1. Wooded canyon on U. S. 40 east of Salt Lake City, June 30, 1939, 20204. 2. Roadside in Little Cottonwood Canyon near its mouth, June 30, 1939, 20202. 3. Moist woods along stream, Tanners Flat, Little Cottonwood Canyon, June 30, 1939, 20203. 4. Moist woods along stream, American Fork Canyon 5 miles from its mouth, July 1, 1939, 20210. COLORADO: 1. Scattered in spruce woods, alt. about 8000 ft., Rabbit Ear Pass, 14 miles southeast of Steamboat Springs, July 3, 1939, 20195. 2. Roadside and wooded bank, 9 miles south of Steamboat Springs, July 3, 1939, 20196. 3. Gorge below Fish Creek Falls, Steamboat Springs, July 3, 1939, 20193. 4. Open woods at camp ground, Fish Creek Falls, July 3, 1939, 20197. 5. In woods along road to Fish Creek Falls, July 3, 1939, 20194. 6. Moist shady hillside, alt. 10,000 ft., Conejos River Canyon, July 24, 1938, *Francis Ramaley 15672*. 7. Open aspen forest, well-drained soil above the creekbed, Papoose Creek, Yampa River drainage, Rio Blanco Co., Aug. 11, 1938, *F. Ramaley & J. Ewan 16478*. OREGON: 1. McKenzie Pass, July 15, 1939, *Garland M. Powell*. 2. Shaded roadside in "black sand" (stabilized dune area), 1.5 miles northwest of Warrenton, Aug. 9, 1938, *W. T. McLaughlin*. 3. Port Orford, Aug. 12, 1938, *Doris K. Gillespie 15399*. CALIFORNIA: 1. On beach above Meadow Brook public camp, alt. 5600 ft., Brightman Flats, Tuolumne Co., July 16, 1939, *Ira L. Wiggins 9245*. 2. Low dense, more or less ground-cover under trees (*Pinus contorta Murrayana*, *Abies magnifica*, *Lonicera*, *Epilobium*, *Salix*), ¼ mile north-northeast of Silver Lake, El Dorado National Forest, Amador Co., Aug. 28, 1938, *Beryl O. Schreiber 2546*. 3. North Fork San Jacinto River, San Jacinto Mts., Aug. 14, 1938, *Carl Epling*. 4. Fir-spruce association, alt. 1675 m., near head of Nigger Grade, Palomar Mt., San Diego Co., Aug. 4, 1938, *Frank F. Gander 6239*. 5. Eureka, Aug. 6, 1938, *Doris K. Gillespie 15397*. 6. Elk River 6 miles south of Eureka, Aug. 8, 1938, *Gillespie 15398*. 7. Soft chaparral, 1.5 miles southeast of Abbot's Lagoon, alt. 25 ft., Marin Co., Aug. 6, 1938, *Beryl O. Schreiber 2538*. 8. Dense shade, very moist habitat, woodland, alt. 100 ft., First Valley, Inverness, Marin Co., Aug. 7, 1938, *Schreiber 2539*. 9. Among scattered dense clumps of *Polystichum munitum* in predominantly grassland areas, alt. 25 ft., 2.5 miles north-east of Point Reyes Lighthouse, Marin Co., Aug. 6, 1938, *Schreiber 2537*. 10. Thickets on north slope of Strawberry Creek Canyon, 0.7 miles above its mouth, 1100 ft. alt., Berkeley, Aug. 4, 1938, *L. Constance 2397*. 11. Along banks of Gazos Creek, about 5 miles inland, San Mateo Co., Aug. 12, 1939, *Ira L. Wiggins 9296A*. 12. Under *Sequoia sempervirens*, ½–1 mile from the ocean, Palo Colorado Canyon, Santa Lucia Mts., about 12 miles south of Carmel, Aug. 7, 1938, *Mildred E. Mathias 1389*.

²⁸ For aid in obtaining a permit to collect specimens in Yellowstone National Park, the writer is indebted to Dr. C. Max Bauer, Park Naturalist, and Mr. C. K. Skinner, Asst. Chief Ranger.

TABLE VI
OCCURRENCE OF FORMS OF TYPICAL *R. PARVIFLORUS*

		<i>Nuttallii</i>	<i>glabrifolius</i>	<i>trichophorus</i>	<i>bifarius</i>	<i>heteradenius</i>	<i>villosus</i>	<i>hypomalacus</i>	<i>adenius</i>	<i>acephalus</i>	<i>micradenius</i>	<i>scopulorum</i>	<i>allocalyx</i>
ONTARIO	1		18		14	1							
	2				2			1					
	3	2	6	2	40								
	4		5		2								
	5		3		4								
	6		8										
	7		1		3								
	8	1	10	1	8								
	9		4		37								
MICHIGAN	1*					20							
	2				20								
	3		2	1	16	1							
	4		3		19								
	5				17								
	6		2		23						1		
	7			1	13	2							
	8				6	1							
	9		6		23						5		
	10		3		27			4					
	11		11		29								
	12		4	1	15								
	13				23								
	14		1		14								
	15		12		13							2	
	16		2		28						2		
	17		1		46			1			2		
	18		5		15								
	19		2		13								
	20*				12								
	21		5		4								
	22*				12								
	23		1	1	14								
	24		10		74			1					
	25†				13								
	26		2	1	25							1	
	27		3		14								
WISCONSIN	1		2		4			2					
	2		3		5								
	3		2		19								
	4				18			4			2		
	5		1	1	15						1		
	6		9		10								
	7		2		7	1		1					

* This collection appears to consist of one clone, and does not enter into the data for maps 20-23.
† This collection was made all from one clone, and does not enter into the data for maps 20-23.

TABLE VI (Continued)

		<i>Nuttallii</i>	<i>glabrifolius</i>	<i>trichophorus</i>	<i>bifarius</i>	<i>heteradenius</i>	<i>villosus</i>	<i>hypomalacus</i>	<i>adenius</i>	<i>acephalus</i>	<i>micradenius</i>	<i>scopulorum</i>	<i>allocalyx</i>
WISCONSIN	8				19			1					
	9		1		22	1		1	1				
	10				3			6					
	11		1		19								
	12				8								
	13				14			2					
	14							13					
	15*				10								
	16*				13								
	17		3		7								
	18		6	4†	33	1		1			3	1	
	19		3	3	15	2					1		
	20		7		1								
MINNESOTA	1*				21								
	2		2		12								
	3		14		4	1		1					
	4		5	1	30	1		1					
	5		2		30	1						1	
	6		2		11						1		
	7				16			1			1		
	8		9		8			1					
SOUTH DAKOTA	1		5									20	
	2		3									3	
	3	2	5									5	
	4		20									8	
	5		6								1	21	
	6											9	1
ALBERTA	1		5									15	
	2	1	10		13						3	2	
	3		17									19	
	4		10		2						1	11	
MONTANA	1*											47	
WYOMING	1		8										
	2		18	2									
	3		4										
	4	5	32									6	
	5											10	
UTAH	1											5	
	2		22										
	3		2									30	
	4	2	14	4	28	3							

* This collection appears to consist of one clone, and does not enter into the data for maps 20-23.
† Two of these have villous pedicels, which have been found elsewhere only in var. *velutinus*.

TABLE VI (Continued)

		<i>Nuttallii</i>	<i>glabrifolius</i>	<i>trichophorus</i>	<i>bifarius</i>	<i>heteradenius</i>	<i>villosus</i>	<i>hypomalacus</i>	<i>adenius</i>	<i>acephalus</i>	<i>micradenius</i>	<i>scopulorum</i>	<i>allocalyx</i>
COLORADO	1	1										3	1
	2		20									3	
	3		10		1						8	21	
	4		14									12	
	5		3								2	19	
	6										1	1	
	7		3										
OREGON	1				7								
	2		4		20								
	3				10		5		10				
CALIFORNIA	1		21										
	2										14		
	3				20		4	4					
	4*				4		4	9					
	5†										2		
	6‡				10			2			4		

* This collection also contains one individual of var. *velutinus*.
† This collection also contains 25 individuals of var. *velutinus*.
‡ This collection also contains 12 individuals of var. *velutinus*.

5. IS *R. parviflorus* A PREGLACIAL RELIC ABOUT THE UPPER GREAT LAKES?

The initiation of the present study was an attempt to combine two ideas. The first, published by Professor Fernald,²⁹ was expressed as follows: "The high bluffs of Keweenaw evidently were not denuded by Wisconsin ice and, consequently, they served as centers on which many species survived . . . , some later to spread slightly to lower levels and, in case of readily dispersed species, like *Rubus parviflorus* . . . , to extend over much of the Upper Lakes region . . . " The second, elaborated by Dr. Sewall Wright and others, has been expressed by Dobzhansky³⁰ in the words: "A finite population left to its own devices must, therefore, suffer a progressive decay of its hereditary variability and sooner or later must reach a complete genetic uniformity." Again,³¹ "The

²⁹ *L. c.*, p. 216.
³⁰ *Genetics and the origin of species*, p. 130. 1937.
³¹ *Ibid.*, 132.

TABLE VII
OCCURRENCE OF FORMS OF *R. PARVIFLORUS* VAR. *VELUTINUS*

	<i>paratrichophorus</i>	<i>parbifarius</i>	<i>parvillosus</i>	<i>parahypomalacus</i>	<i>praebifarius</i>	<i>isohypomalacus</i>	<i>paramicradenius</i>
CALIFORNIA 4*		1					
5†	5	6			12		2
6‡		6			5	3	
7	4	5	3	14			
8		25		3¶			
9	5		3				
10		42					
11§	32						
12	36	16					

* This collection also contains 17 individuals of typical *R. parviflorus*.
† This collection also contains 2 individuals of typical *R. parviflorus*.
‡ This collection also contains 16 individuals of typical *R. parviflorus*.
¶ Some pedicels bear only short-stalked glands; others in the same inflorescence bear long-stalked glands.
§ Inflorescences 1-few-flowered with long pedicels, resembling but more extreme than those illustrated for var. *parviflorus* (Fernald, l.c., plate 365, fig. 1).

smaller the population size, the more rapid is the scattering of the variability and the eventual attainment of genetic uniformity.”

If, then, *Rubus parviflorus* was once confined for a long time on one or few nunataks about Lake Superior it should show less variation in that region than in some other parts of its range. Actually this proved to be only partially the case. In so far as variation is expressed in the number of forms in each region, as listed in tables VI and VII, it is just as variable in Wisconsin as in California, and in Michigan as in Colorado. But while the number of forms is about the same in each region, their proportions differ from region to region. A study of the proportions of individuals displaying each character, in each region, shows that the loss of variability by the suppression of minority characters has gone a little farther in the Great Lakes region than elsewhere. This is expressed mathematically in table IX, page 344.

While the range and amount of variation are about the same in all regions, the number of forms varies greatly from colony to colony within each region. This may be seen in table vi under Ontario, where collections 2-8 are all from the vicinity of Meldrum Bay, and the number of forms in each collection varies from one to four. The number of forms in any colony is not entirely a factor of the age of the colony, in the sense discussed by Dobzhansky, but depends, as in *R. odoratus* (see page 307), on how many seeds started the colony and whether the colony has increased in size by vegetative spread or by seed reproduction.

While *R. odoratus* grows most commonly on recently cut soil, *R. parviflorus* does not have this soil preference. In regions where the climate is favorable (this factor will be discussed later) it forms a solid growth along the roadside (beautifully pictured by Fernald, *l. c.*, pl. 363) and also occurs as scattered stems, connected by rootstocks, in thick woods. In places where a road cuts through woods, the writer has tried unsuccessfully to determine whether the plant had established itself along the roadway and spread into the woods, or was originally scattered in the woods and had expanded along the roadway (pl. 9, fig. 1). In either case, and whatever the period of occupancy of the Upper Great Lakes area, the entire *R. parviflorus* population of that area appears to be functioning as one breeding unit rather than as many isolated units. In map 22 the collections about the Great Lakes have been grouped into regions and a pie-diagram made for each region, just as was done for *R. odoratus*, except that now 6 characters are used instead of 4 as in the eastern species; the diagrams for the six regions in map 22 show close similarity, as do those in the southern part of the glaciated territory in map 3, rather than the dissimilarity shown in the unglaciated parts of map 3.

In map 20 the stations listed in table v, shown by solid dots, have been grouped into seven regions; each region has been demarked by a line and given a name. From the data in tables vi and vii a pie-diagram has been made for each region. These pie-diagrams show the plants of the Coast Ranges of California to be very distantly related to those of all the other

regions: this is consistent with the taxonomic treatment of the plants of the Coast Ranges as a separate variety. Also evident is the rather close resemblance among the four central regions of Alberta, Wyoming, Black Hills and Colorado. Less to be expected is the resemblance of the Great Lakes region to the Sierra region. The significance of this will be pointed out below.

From the figures in the pie-diagrams the averages of differences of percentages between regions have been computed in the way described on page 311. Table VIII shows the averages of

TABLE VIII
AVERAGES OF DIFFERENCES OF PERCENTAGES BETWEEN REGIONS

	Great Lakes	Black Hills	Wyoming	Alberta	Colorado	Sierra	Coast Ranges
Great Lakes	—	33	19	25	30	8	41
Black Hills	33	—	15	8	3	25	68
Wyoming	19	15	—	8	12	14	53
Alberta	25	8	8	—	5	17	61
Colorado	30	3	12	5	—	23	66
Sierra	8	25	14	17	23	—	43
Coast Ranges	41	68	53	61	66	43	—

percentages of differences between all regions, and many of these are also shown on maps 20 and 21 by large figures superposed on heavy lines connecting regions. Lower numbers indicate closer relationship, and these figures bring out more positively the observations of the preceding paragraph.

On map 21 are shown only the average percentage differences of less than 10. Again the close relationships are emphasized, one of the Rockies and the Black Hills, and the other of the Great Lakes and the Sierra region.

It is this latter fact which appears to the present writer as of great importance in the consideration of the claim of *Rubus parviflorus* to the title of preglacial relic in the Middle West. If the great gap in its range (see map 24) has been due to a former continuous range having been bisected by ice-sheets between Lake Superior and the Black Hills, these two regions could be expected to show a close relationship. On the contrary, the relationship between these two regions appears on map 20 as remarkably remote. The Great Lakes region shows much closer connection with the region along the Pacific coast (Oregon) and inland California; this connection, since it was not across Wyoming, Colorado, or the Black Hills, was presumably across a more northern region. Before discussing this possibility it is necessary to determine what ecological factors influence the range of this plant.

Map 25 shows the range of *Astragalus caryocarpus*, a characteristic plant of prairies and plains. On the same map are shown the maximum extent of Pleistocene glaciation, and the Fall Line, but there is no obvious relationship between either of these and the range of the plant. Comparison with map 26, however, shows the correlation of this range with provinces of low humidity. It may now be observed that the range of *Astragalus caryocarpus* almost exactly FITS INTO THE GAP in the range of *Rubus parviflorus* (map 24). If both are controlled by one factor, the reaction of one plant is positive, that of the other negative. The range of the *Astragalus* is correlated with aridity; is that of the *Rubus* correlated with humidity?

Definitely, it is. Figures for a suitable portrayal of regions on a basis of humidity are not available, and if they were they would not include the microclimates so important in plant distribution. But some facts are clear without figures, and the following personal observations have convinced the writer of the dependence of *Rubus parviflorus* on a relatively high humidity and low summer temperature.

On the north shore of Lake Superior, in Minnesota, the Thimbleberry is an aggressive plant, occurring not only in woods and openings along the shore and in canyons entering

the lake, but as a common weed in many places. Particularly vivid was the experience of Dr. J. T. Curtis and the writer at Lutsen, where we were able to follow the elusive overgrown old lumber roads, only by the still persistent line of Thimbleberry (pl. 9, fig. 2). It has similar weedy habits near the shore of Bayfield County, Wisconsin, on the Apostle Islands, and in the Porcupine Mountains and on Keweenaw Point in the Upper Peninsula of Michigan. On Keweenaw Point it grows in the towns, forming a hedge between houses (pl. 10, fig. 3).

Inland the aggressiveness decreases. While it is apparently adventive along the Gunflint Trail going north from Grand Marais, Minnesota, it seems to be almost absent north and west of Duluth. This seems to be due partly to the slightly warmer area north of Duluth (map 27) and even more to the dry west winds of this region (map 28).

In northern Wisconsin the southern limit of Thimbleberry is near the 66° July isotherm (map 27). In the canyon of Manitou Falls about 15 miles south of Superior, Wisconsin, it barely exists; it was possible to find only eight scattered and dwarfed flowering individuals. Likewise in Vilas County, Wisconsin, it is uncommon and usually not aggressive, although Dr. Curtis reports a thrifty colony at Jute Lake. In the more southern stations in Wisconsin it is confined to the heavier soils, while nearer Lake Superior the soil preference is scarcely marked.

In Door County, Wisconsin, the Thimbleberry is rare on the Green Bay side of the peninsula, but on the Lake Michigan side it makes an almost solid growth, as is shown on map 27. Its aggressiveness well south of the 66° July isotherm is due to local conditions. Mr. Eric R. Miller, Meteorologist in Charge of the United States Weather Bureau at Madison, to whom I am also indebted for assistance in procuring the data from which maps 27 and 28 were drawn, tells me that the west side of Door County peninsula is warmed by the southwest winds which follow Green Bay, whereas the east side of the peninsula is cooled by proximity to Lake Michigan; this difference in temperature is not shown by readings from one station at the

tip of the peninsula and another near its base, but is noticeable when one drives across the peninsula. In the local cool zone along the Lake Michigan shore the saturation deficit would be lower even if the relative humidity were the same on the two sides, which it probably is not, due to frequent fog on the lake and local breezes from over the water.

Dr. R. F. Griggs has recently called attention to the concentration of rare plants, many of them considered by some botanists to be preglacial relics, on islands and peninsulas,³² and in telling of the weedy tendencies of some of these plants he specifically mentions *Rubus parviflorus* in Keweenaw.³³ It is weedy in Keweenaw Point because on the peninsula it is favored by low temperature (map 27) and by the prevailing west winds (map 28) blowing across the lake and carrying moisture. It is also weedy along the Minnesota shore of Lake Superior where the atmosphere is cool and moist, and this weedy tendency is carried inland in the Arrowhead of Minnesota to a limited degree. On the Apostle Islands at the tip of Bayfield County, Wisconsin, and to a slightly less extent on the adjacent mainland, the Thimbleberry is rather aggressive in following roadsides and woodland trails. This is true also in the Porcupine Mountains and about Ontonagon, Michigan. In Door County, Wisconsin, as already mentioned, conditions on the two sides of the peninsula make the plant rare on one side and very abundant on the other.

Elsewhere in its range in the Lake states the Thimbleberry tends to grow on roadsides and along margins of woods, but it is scarcely aggressive or abundant; its normal weedy propensities are curbed by the absence of completely favorable atmospheric conditions.

I do not understand the distribution north of Lake Huron. On the peninsula of Bruce County, Ontario, the Thimbleberry is very rare, and I have seen it only in woods near Cameron Lake. It is abundant about Meldrum Bay at the west end of Manitoulin Island and occurs in open ground on St. Joseph Island southeast of Sault Ste. Marie. I have traversed much

³² Bull. Torr. Bot. Club 67: 589. 1940. ³³ *Ibid.*, p. 583.

of the shore line of Bruce Peninsula, of Manitoulin Island, of St. Joseph Island, and of Drummond Island, and while of course a statement that it is not present except as shown on map 27 would be too sweeping, it is certainly absent in many localities apparently as suitable as those in which it is abundant farther west, and seemingly just as favorable as the few spots where it is found. Perhaps it is just in the process of spreading into this region and grows where seeds have happened to land.

There appear to be no collections from the north side of the Upper Peninsula of Michigan between Sault Ste. Marie and Munising. I have not collected along this shore except at Brimley, 15 miles west of Sault Ste. Marie, where the red clay banks would seem favorable for Thimbleberry, but none was found.

In the summer of 1939 I went as far west as Utah and Colorado for the specific purpose of collecting quantities of this plant. The eastern botanist traveling for the first time from southern Wisconsin across Minnesota and South Dakota to the Black Hills will soon abandon the idea that glaciation accounts for the absence in these regions of various species common in the eastern forests. Even if he has been familiar with rainfall maps, etc., he will not fail to be impressed by driving hours on end through progressively treeless plains, and then for mile after mile in a monotony of cactus and sagebrush. But on reaching the Black Hills, he will find again a region of forests, streams and swamps, of brook trout and beaver, and of such familiar eastern mesophytes as ostrich fern, bloodroot, columbine, dwarf Solomon-seal, etc.³⁴ In the cool and moist canyons of the northern Black Hills the Thimbleberry grows; Dr. Hayward's paper brings out its ecological relationships in his illustrations. His Fig. 7 shows Spearfish Canyon, which supports a heavy stand of white spruce with quantities of Thimbleberry; this is characteristic of a small region surrounded by country pictured in his Figs. 8-11, where the absence of Thimbleberry can by no means be attributed to glaciation.

³⁴ Cf. Hayward, H. E. Bot. Gaz. 85: 353-412. 1928.

To the easterner visiting the western states for the first time the conditions about Salt Lake City are most striking. Rising from the arid plains and bordering the Wasatch Range are the terraces of Lake Bonneville, impressive evidence of a once great body of water. On the parched sides of the Wasatch Range are sagebrush, shadscale, rabbitbrush and greasewood (pl. 11, fig. 5), but in the canyons are heavy forests and rushing streams of icy water from the snowfields above—one might almost be persuaded that he is back in Glen Ellis in the White Mountains. It is in these cool moist canyons that the Thimbleberry grows (pls. 11-12, figs. 6, 7). The occurrence of Thimbleberry in mountainous areas and its absence in intervening lowlands is shown in map 36.

These observations convince the writer that the gap in the range of *Rubus parviflorus* is due to aridity and not to glaciation.³⁵ It is easy to concur with Professor Fernald's statement,³⁶ "it seems quite illogical to argue that such species . . . have been arriving in post-Wisconsin times from different remote centers outside the area of general Pleistocene glaciation . . ."; the cross-continental migration must have been ancient, even if postglacial. In the same paragraph he expresses doubt that they could have made this migration "without leaving in their long hypothetical cross-country journeys a somewhat continuous train of intermediate stations." Had he said "more or less continuous" it would have been easier to agree, for the intermediate stations are "more" for some species and "less" for others. They are *less* continuous for *Polystichum Lonchitis* (207),³⁷ *Ceanothus sanguineus* (210), *Vaccinium membranaceum* (211), *Adenocaulon bicolor* (213) and many others, and for some other species they are *more*. Some of these other species will be discussed in the next paragraph.

³⁵ This statement is deliberately worded to refer to one species and one alone. Professor Fernald points out (*l. c.*, pp. 212-213, 217-218) that both mesophytes and xerophytes show this gap in their ranges. The present investigation concerns but one species and the conclusion is that *that* species is not a preglacial relic.

³⁶ *L. c.*, p. 208.

³⁷ Figures refer to the page numbers where these are mapped in Professor Fernald's paper.

Hultén decries³⁸ the practice of basing conclusions exclusively on extreme types of range, as follows: "When tackling the problems offered by the geographical areas of plants, many authors have chosen to discuss peculiar or singular types having a distribution out of the common, in the hope that they will suddenly give a clue to the solution of the problem. . . . It is surely more rational to start the investigation with the simplest types, those that show the least possible peculiarities. When they have been interpreted, the complicated and often strongly interrupted areas of the singular or peculiar types are likely to be better understood."

Populus balsamifera (map 29) has a broad range across the northern part of the continent, chiefly in glaciated regions; this range seems obviously to have been attained in postglacial time. The same is true of *Picea glauca* (map 30), but its southward extension down the Rockies and into South Dakota has been lost, leaving outliers in the Black Hills and in Montana. The range of *Arabis divaricarpa* (map 31) is becoming definitely pinched in the region northwest of Minnesota. This trend has resulted, in *A. Drummondii* (map 32), in a breach between the eastern and the western parts of the range, with a few scattered intermediate stations—this is one of the *more* species of the preceding paragraph. An even wider gap appears in *Botrychium Lunaria* (map 33), but comparison with map 29 shows how a distribution like that of the *Botrychium* might have been derived from one like that of the *Populus*. If the derivation was of this nature, and the distribution of the *Populus* is clearly postglacial, then the range of the *Botrychium* is postglacial also. It is a short step from a range like that of *Botrychium Lunaria* to one like *Rubus parviflorus* (map 34), whose occurrence east of the Rockies has been reduced to the Black Hills and the vicinity of Lakes Superior, Michigan and Huron.

Perhaps it is dangerous to imply that the various gaps in the ranges shown in maps 29–34 are due to the varying toler-

³⁸ Outline of the history of Arctic and boreal biota during the Quarternary period, pp. 9–10. 1937.

ance of the low humidity in the region between the Great Lakes and the moist ravines of the western mountains, since a decreasing tolerance of low humidity shown by these species is not easily demonstrated experimentally. However, it is not necessary to explain to a botanist familiar with the northern states and southern Canada that balsam poplar and white spruce are found in a greater variety of habitats than is Thimbleberry. While the former is by no means rigid in its requirements, it does need a comparatively cool, moist climate. In the Middle West, wherever Thimbleberry grows, white spruce ordinarily grows also, but where white spruce grows Thimbleberry does not necessarily accompany it. The limiting factors of the Thimbleberry are the same as those of the white spruce, but to a greater degree.

When, then, did the Thimbleberry spread from the western regions to the Great Lakes? At some time when the climate was sufficiently cool and moist for white spruce to spread from coast to coast, and south to the Black Hills. Perhaps this was while glacial influence was still felt³⁹; perhaps it was during some later humid period. It may be significant that in spite of the large number of eastern woodland species isolated in the Black Hills there has not been described a single endemic variety of an eastern species from that region. These species must, then, have entered the Black Hills fairly recently. And conditions which would permit plants like bloodroot to spread westward to the Black Hills might also permit a migration of Thimbleberry eastward along a more northern route.

Rubus parviflorus did not populate the Black Hills from the same stock as that which reached the shores of the Great Lakes.

³⁹ "The glaciations were connected with such great changes in climate that it is unthinkable that the Great Basin should not be influenced by them. Low temperature checking evaporation probably made itself felt when the ice-sheet began to grow in Canada. Later also precipitation must have become greater. These cooler and moister conditions, begun at an early stage of the glaciations, gradually increased, and the highest point of moisture was reached during the pluvial periods which seem to have been a consequence of the great climatic change which checked the further expansion of the ice-sheets and caused their disappearance." Antevs, Ernst. On the Pleistocene history of the Great Basin. Carnegie Inst. Wash., Publ. No. 352: 74. 1925.

The Thimbleberry population of the Black Hills was derived from the Rocky Mountains; map 21 shows the close relationships within the regions designated as Alberta, Wyoming, Colorado and the Black Hills. The stock which spread into the Middle West must have existed to the northward, and have spread southeastward at about the same time it migrated southwestward along the Pacific coast to northern California and down the Sierras, for the populations of this far western region are closely similar to those of the Middle West (map 21).

The amount of variation of *R. parviflorus* in the Great Lakes area as compared to that in the western parts of its range has already been mentioned (page 333). Qualitatively the variation is the same in both regions, for the same forms are found in each. Quantitatively, however, variation in the Great Lakes area is less than elsewhere. This is shown by the pie-diagrams on map 20. The diagram for Great Lakes shows, in sector B, that 93 per cent of the individuals have glands on the pedicels 0.5–1.0 mm. long; this indicates that the population is within 7 per cent of uniformity on that character. Figures of 38 per cent in the Black Hills, 42 per cent in Colorado, etc., show much less approach to uniformity. Figures approaching 100 per cent or 0 per cent both indicate a corresponding approach to uniformity, while figures approaching 50 per cent indicate more variation. It is possible to average the amount of deviation from uniformity in all characters shown by the population of a region. For the Black Hills region, for example, this is obtained by averaging the following: 1 from sector A (for 99 per cent deviates from 100 per cent, or uniformity, by 1), 38 from sector B (38 per cent deviates from 0 per cent, also uniformity, by 38), 38 from sector B (62 per cent deviates from 100 per cent by 38), 3 from sector D, and 0 from sectors E and F. This average (1 plus 38 plus 38 plus 3 plus 0 plus 0, divided by 6) is 13, the variability index for the Black Hills. If the population of a region were uniform in all characters, the figures in each sector would all be 100 or 0, and the variability index would be 0. In a population showing maximum variation, half

the individuals with glabrous leaves and half with velvety leaves, and a similar equal division in each of the other sets of characters, the variability index would then be 50.

TABLE IX
VARIATION INDEX OF EACH REGION

Great Lakes	3
Black Hills	13
Alberta	19
Wyoming	13
Colorado	16
Sierra	11
Coast Ranges	12

Table ix shows the same facts that a comparison of the pie-diagrams on map 20 shows visually: the population of the Great Lakes area has less variation than that of any other area.

This small amount of variation, or close approach to uniformity, indicates, according to the ideas expressed by Dobzhansky,⁴⁰ that this population has been at one time much reduced in number of individuals. Here, perhaps, is the only support lent by the present study to the theory that *R. parviflorus* survived glaciation on a nunatak in the vicinity of Lake Superior, for in case of such survival the persisting colony would have been very small and its descendants would lack variation. However, glaciation was not the only event which might have reduced the size of the Great Lakes population. "A late postglacial prehistoric dry period with more widespread drought conditions and more prolonged droughts than at present is definitely indicated by certain bog pollen studies, by soil profile, by the succession in bog profiles, by the absence, or rare occurrence, of many tree, shrub, and herbaceous species from the region of the [Prairie] Peninsula, and by the present distribution of prairie colonies, and prairie species."⁴¹ Such a warm dry period is recorded as having prevailed in Wisconsin, probably not very long ago, and certainly since the third

⁴⁰ See quotations on page 332.

⁴¹ Transeau, *Ecology* 16: 435. 1935.

Wisconsin glaciation.⁴² During such a period the Thimbleberries of the Great Lakes area may well have been temporarily reduced to a very small population.

Ever since they were isolated about the Great Lakes, whether by changes in climate or by glaciation, the Thimbleberries of that region have functioned as but one breeding population. Had they survived on two or more nunataks⁴³ and spread out later so that colonies from the two or more centers merged, the very long isolation as very small populations would have reduced greatly the variation in each colony, with very little chance of each colony retaining the same forms in the same proportions. That this did not happen is shown by the striking uniformity of variations in all the regions about the Great Lakes (maps 22 and 23).

A final word concerning the occurrence of the species in California: var. *velutinus* of the Coast Ranges stands out as distinct from all the other populations (table VII and map 20). It would appear that the Coast Ranges have been continuously humid while other parts of western North America have been experiencing fluctuations in humidity, so that the Thimbleberries have had a continuous existence there for a long time. Aridity at some period separated the race in the Coast Ranges (var. *velutinus*) from the main body of the species. The subsequent readvance in California brought the two races again into contact at the two ends of the Great Valley (map 35, and California collections 4, 5 and 6 in tables IV and V).

SUMMARY

Both *Rubus odoratus* and *R. parviflorus* show variation in the glands and pubescence of calyces, pedicels, petioles, blades and stems. With the exception of *R. parviflorus* var. *velutinus* the various combinations of types of pubescence and glands are treated as forms.

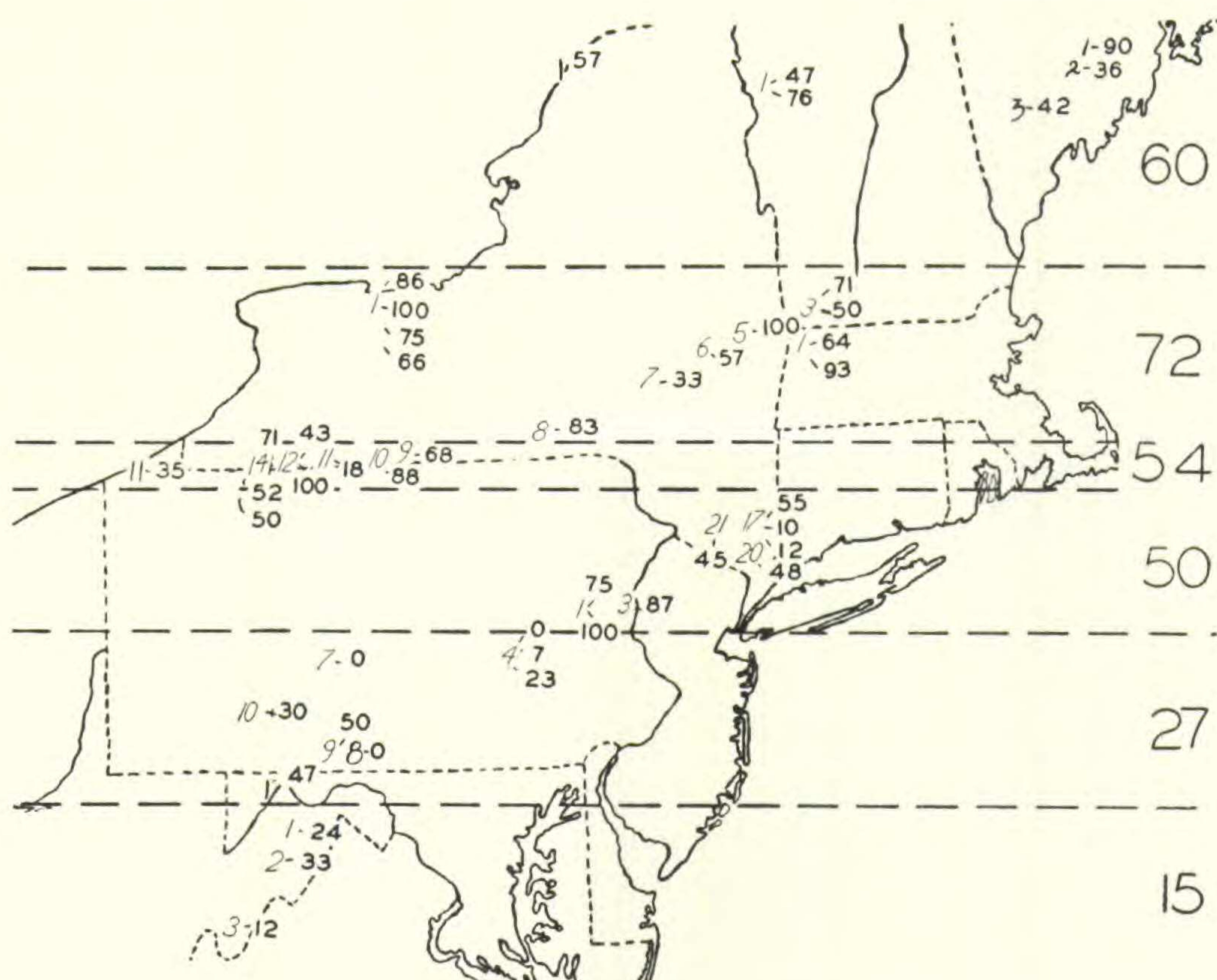
⁴² Truman, Trans. Wis. Acad. 30: 40. 1937.

⁴³ Professor Fernald states or implies the possibility of nunataks in the following regions: Slate Islands (*l.c.*, p. 197), Bruce Peninsula (p. 201), Cloche Peninsula (p. 203), Keweenaw Peninsula (p. 204), and elsewhere (p. 217).

In *R. odoratus* the percentage of individuals with essentially glabrous leaves increases progressively from West Virginia to Maine. The percentages of individuals with a certain type of short-stalked gland on the pedicels does not show such a definite progression. Colonies in regions not glaciated show less resemblance, statistically, than do those in glaciated regions. Colonies in southern Indiana, probably isolated since before the earlier Pleistocene glaciations, show relationship most distant from eastern colonies.

In *R. parviflorus* most of the recently proposed varieties appear invalid, having no definite ranges, occurring intermixed in nearly all colonies, and being founded on combinations of characters which also appear in nearly all possible recombinations. The colonies of the Coast Ranges of California show sufficient isolation of some characters so that var. *velutinus* is maintained for them.

Colonies in the Rocky Mountains show close resemblance to each other in the proportions of occurrence of each character. The colonies about the Great Lakes are more closely related to those of the Oregon coast and the Sierras. It is concluded that the occurrence of the plant about the Upper Great Lakes is due, not to the survival of a preglacial flora on nunataks, but to migration across Canada during a postglacial cool humid period and subsequent bisection of the range by the aridity of the Great Plains.

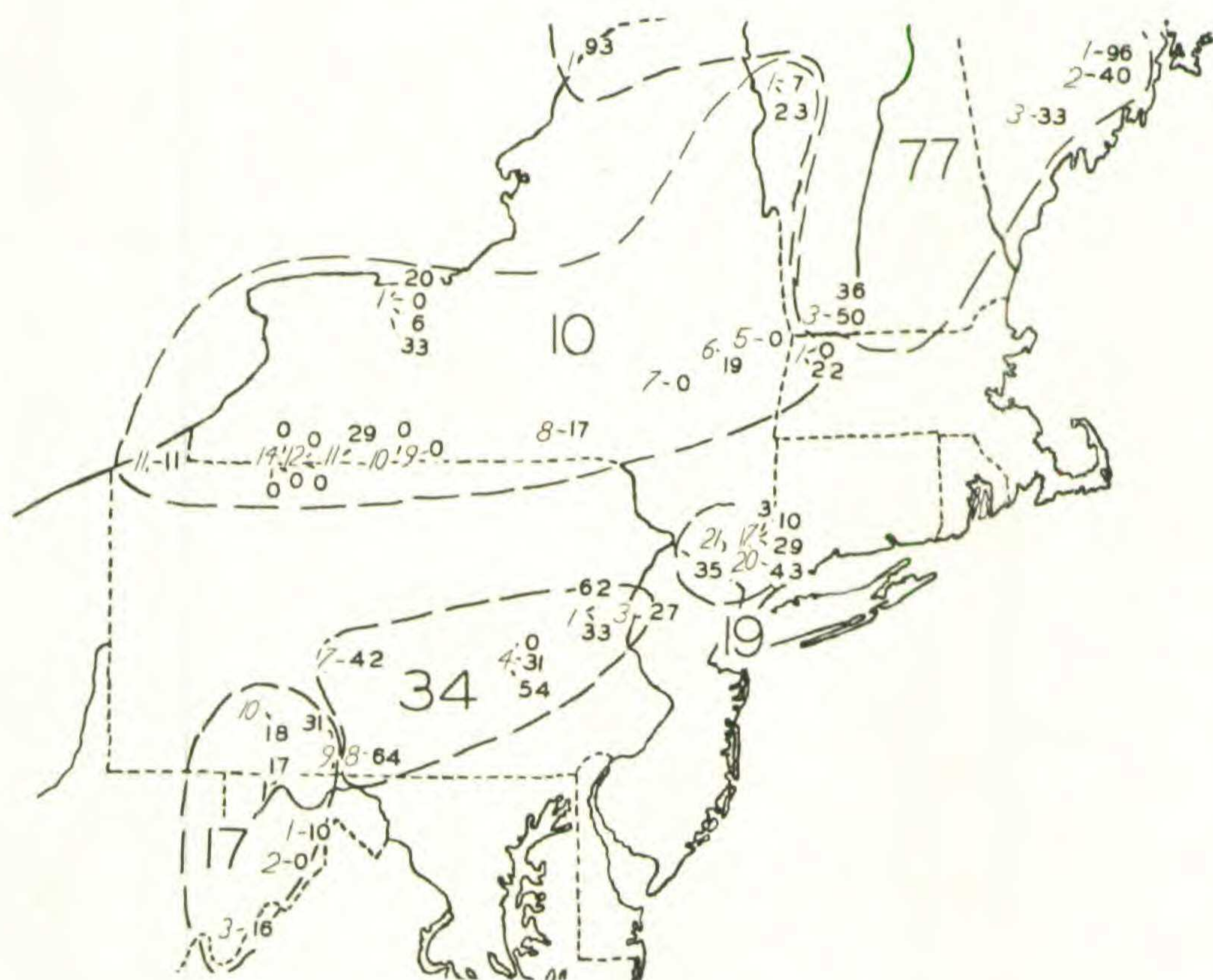


MAP 1

Slanted figures: locations of mass collections. A new series of numbers starts in each state or province.

Erect figures to the right of, or above or below, the slanted figures: per cent of individuals in each collection with leaves glandless above and glabrous or glabrate beneath.

Large figures on right margin: per cent of individuals in each zone (between broken horizontal lines) with leaves glandless above and glabrous or glabrate beneath.



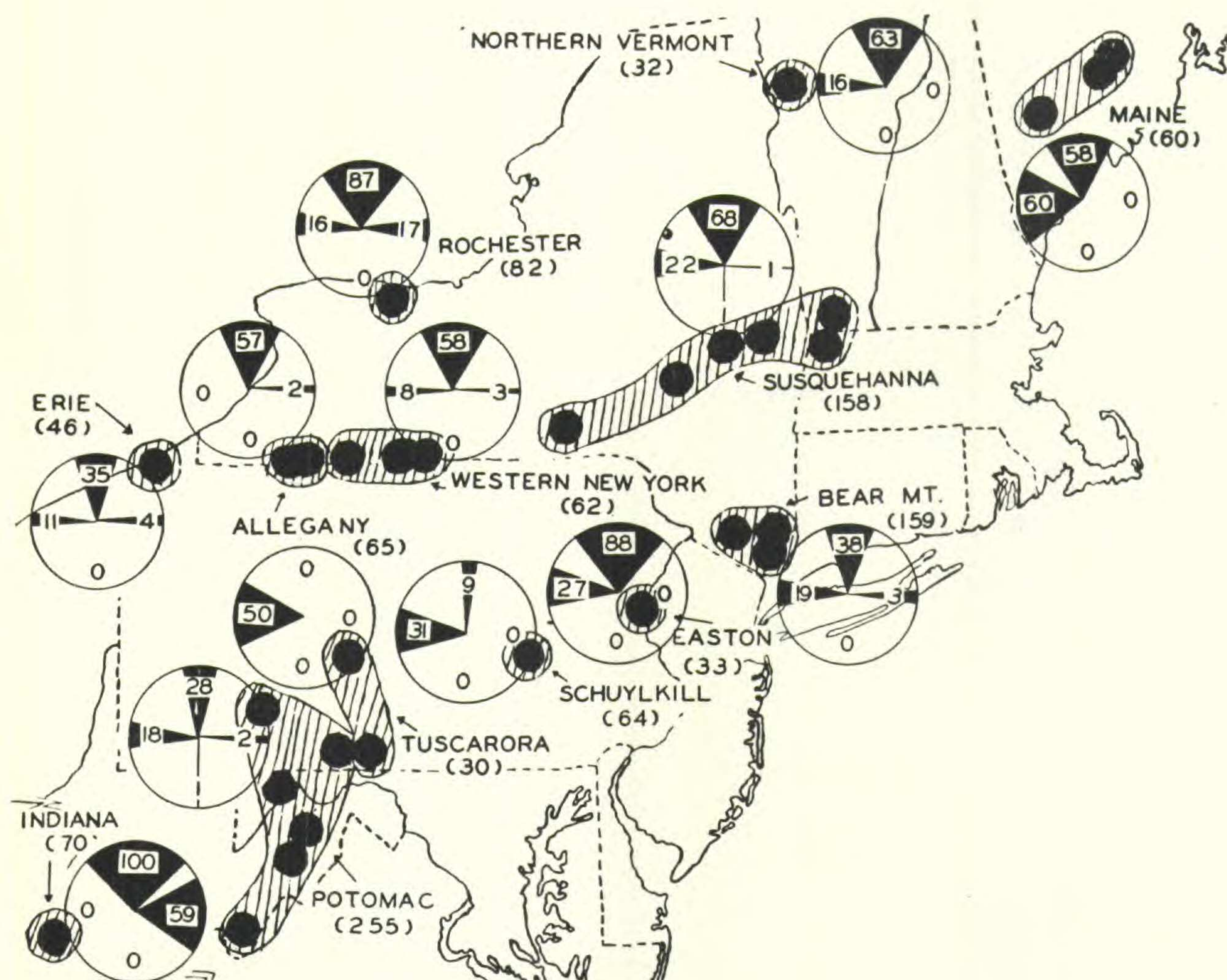
MAP 2

Slanted figures: locations of mass collections.

Erect figures to the right of, or above or below, the slanted figures: per cent of individuals in each collection with glands on the pedicels 0.5-1.0 mm. long.

Large figures: per cent of individuals in each region (enclosed in broken lines) with glands on the pedicels 0.5-1.0 mm. long.

Erratum: Vt. 4—change 50 to 60.

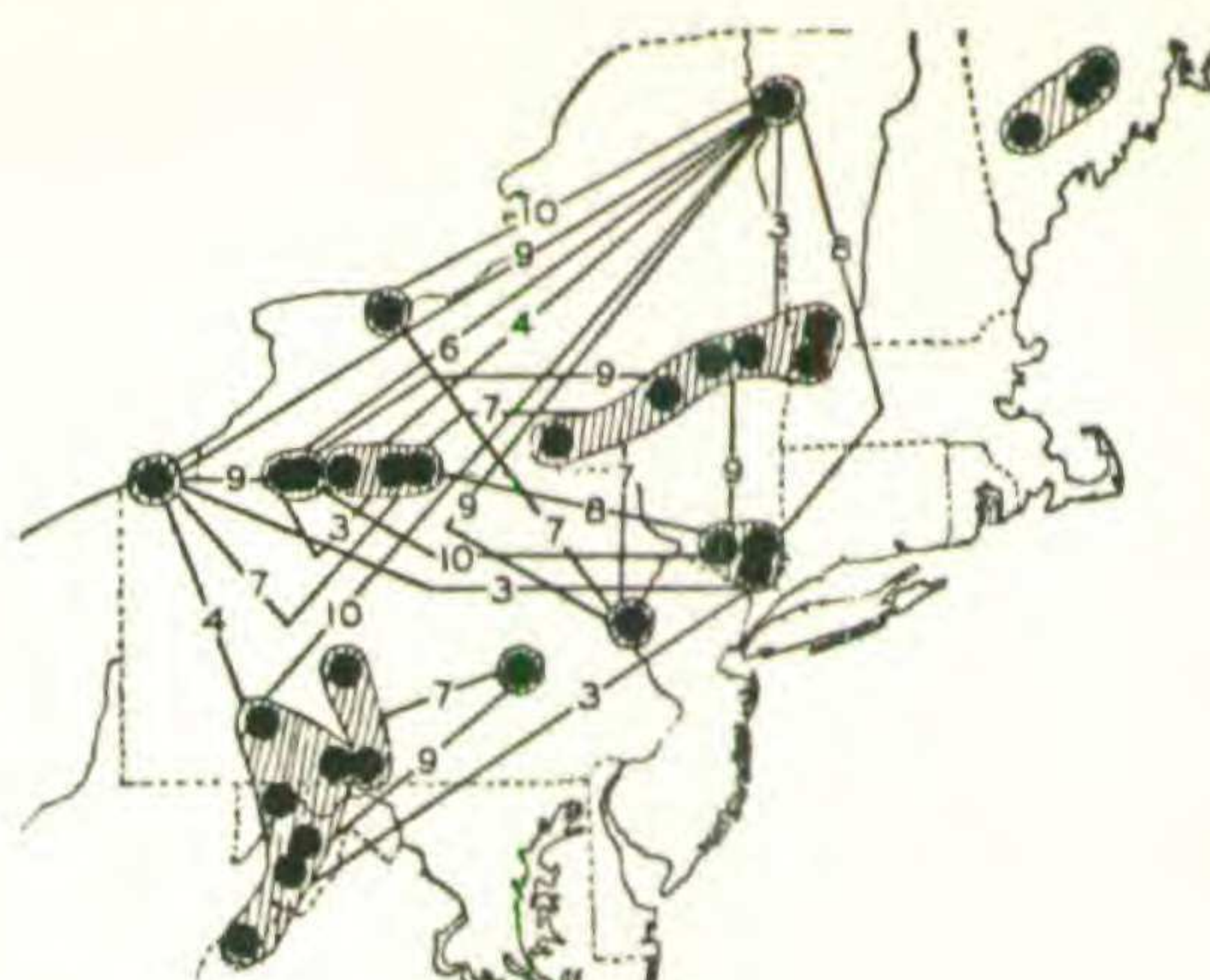


MAP 3

Stations where mass collections have been made (dots) grouped into regions (vertically lined). The figure in parentheses below the name of each region is the number of individuals collected in that region. In the pie-diagram for each region, each sector represents a character, and the figure in the sector shows the percentage of total individuals having this character, as follows: upper sector, per cent of individuals with leaves glandless above and glabrous or glabrate beneath; left sector, per cent of individuals with glands on the pedicels 0.5-1.0 mm. long; lower sector, per cent of individuals with glands of pedicels sessile or subsessile; right sector, per cent of individuals with glands 1.0-2.5 mm. long on the lower sides of veins of leaves. To conserve space, Indiana is inserted in the lower left corner.



MAP 4



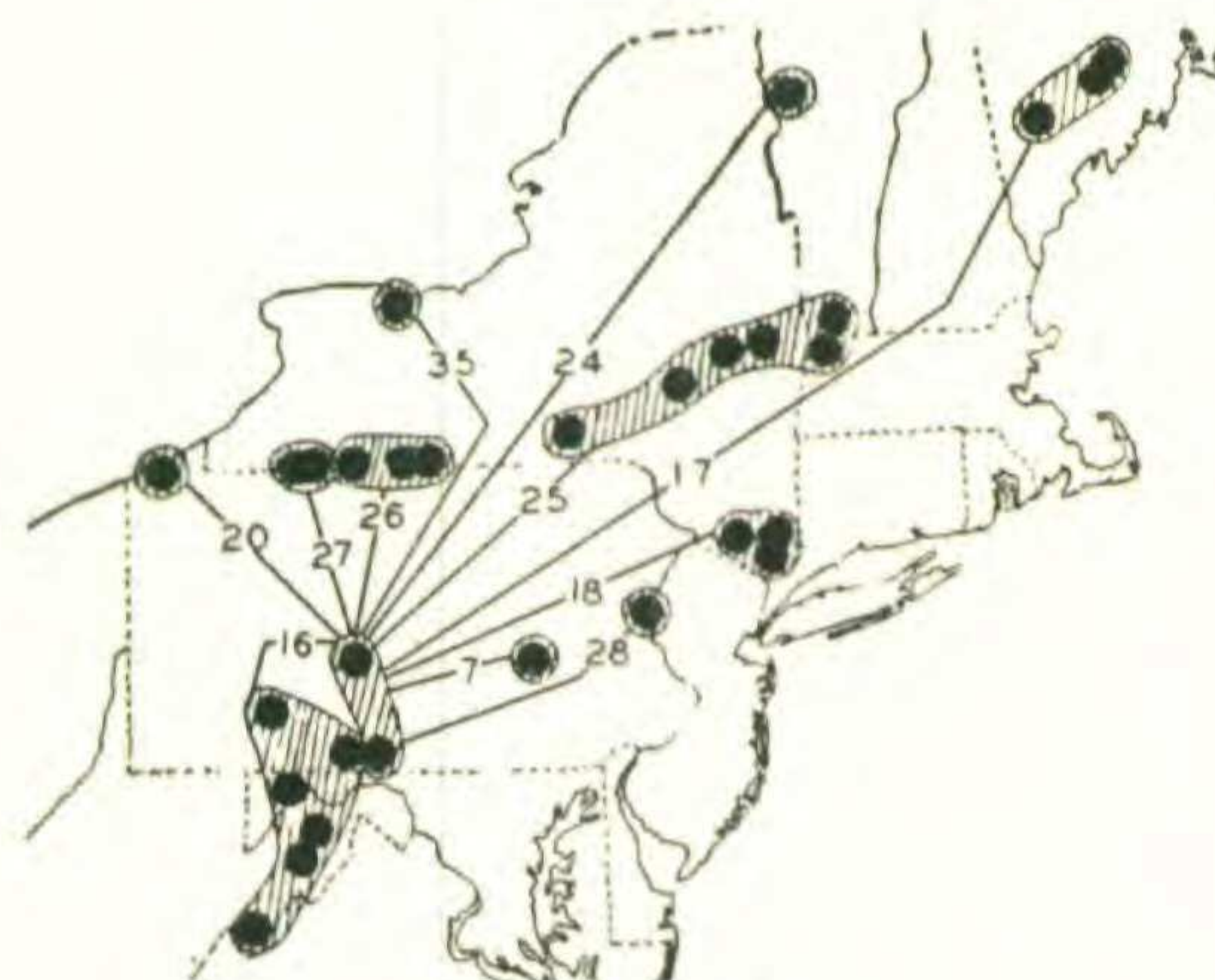
MAP 5



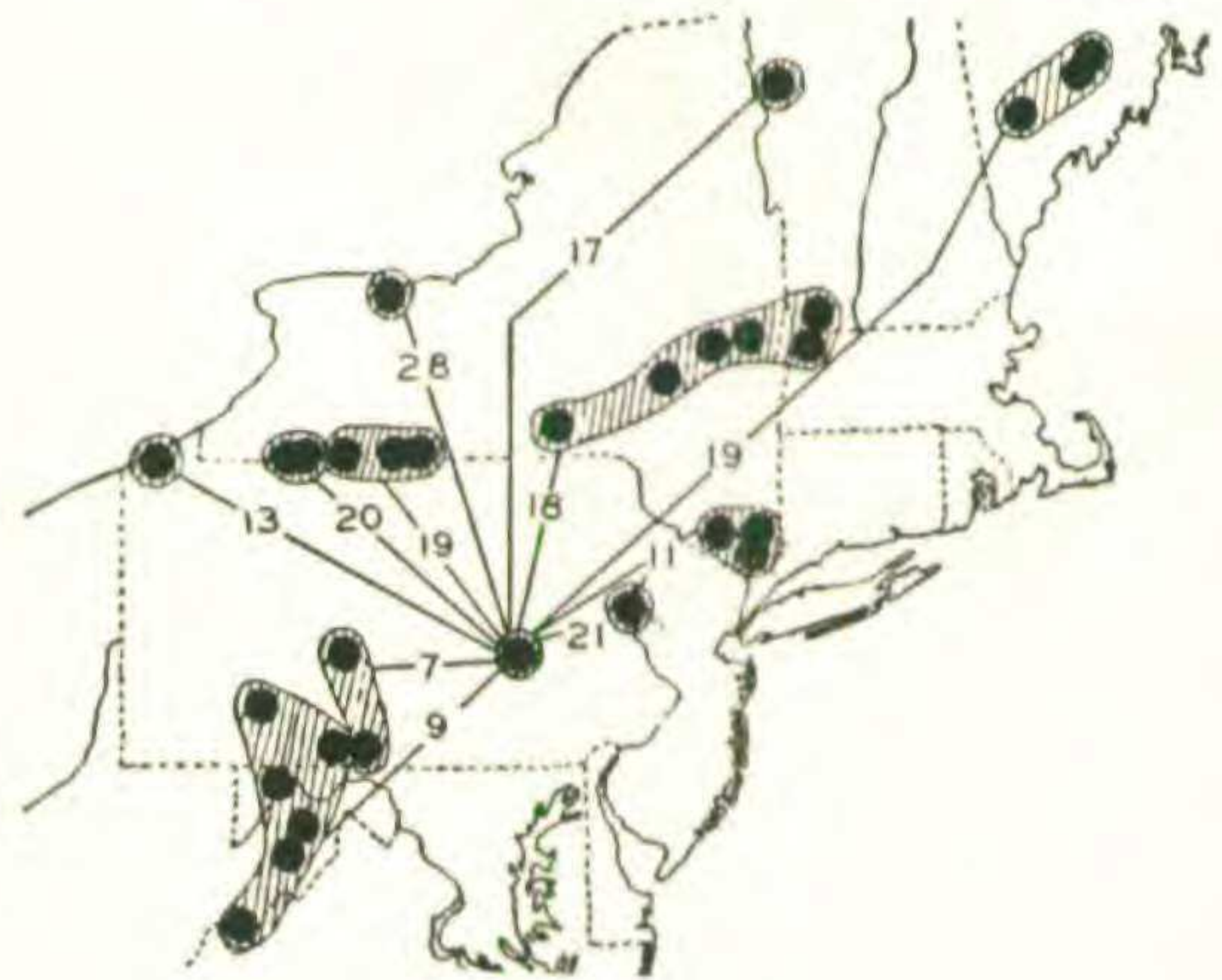
MAP 6



MAP 7



MAP 8



MAP 9

MAP 4. Averages of differences between adjacent regions, derived from map 3; relations between neighboring regions in the more southern post-Wisconsin areas (southern New York State) are close, those between pre-Wisconsin areas (central Pennsylvania and southward) are mostly fairly close, and those between pre-Wisconsin and post-Wisconsin areas are mostly distant.

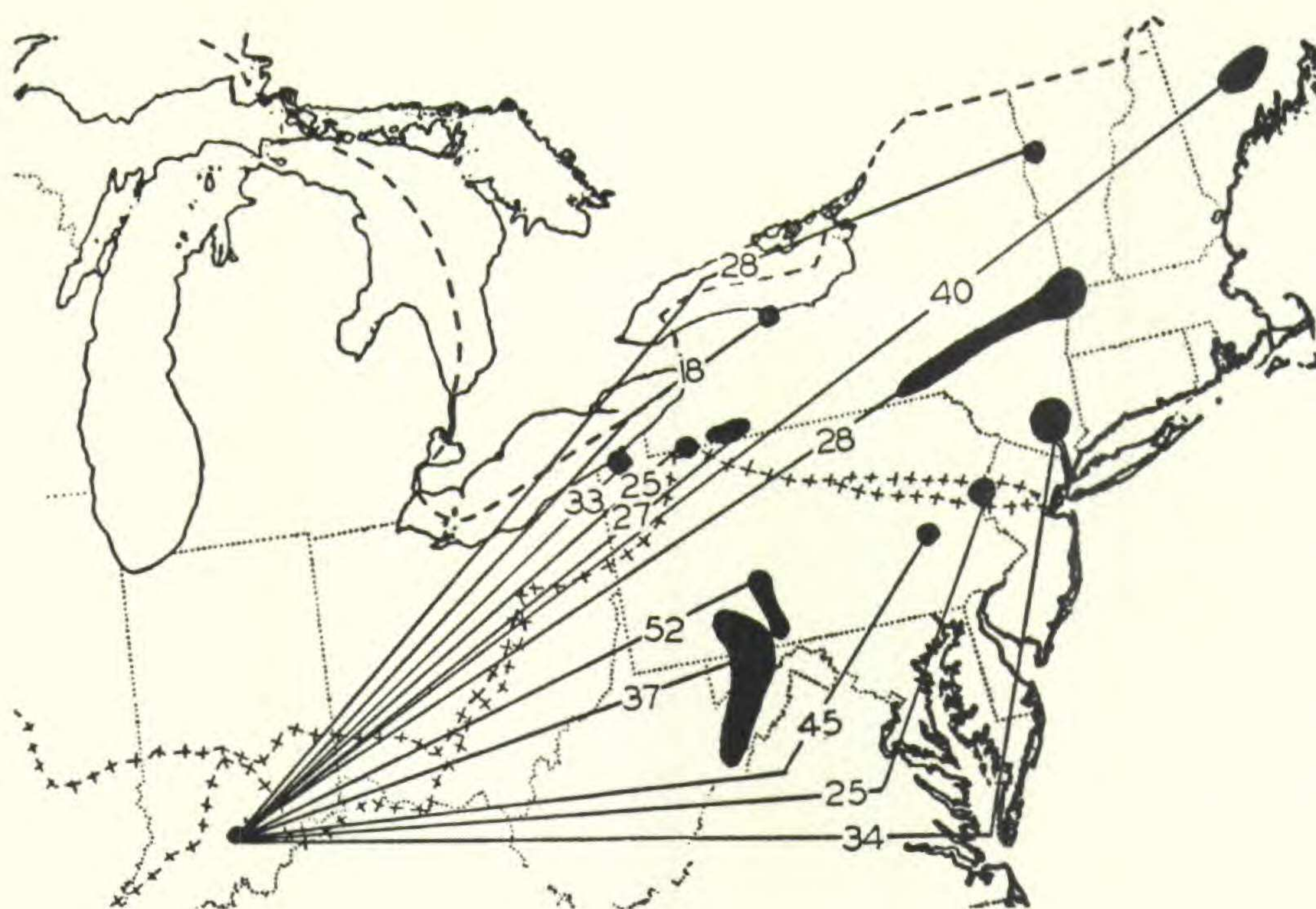
MAP 5. Differences of 10 or less, derived from map 3.

MAP 6. Differences between the Potomac region and other regions, derived from map 3.

MAP 7. Differences between the Eastern region and other regions, derived from map 3.

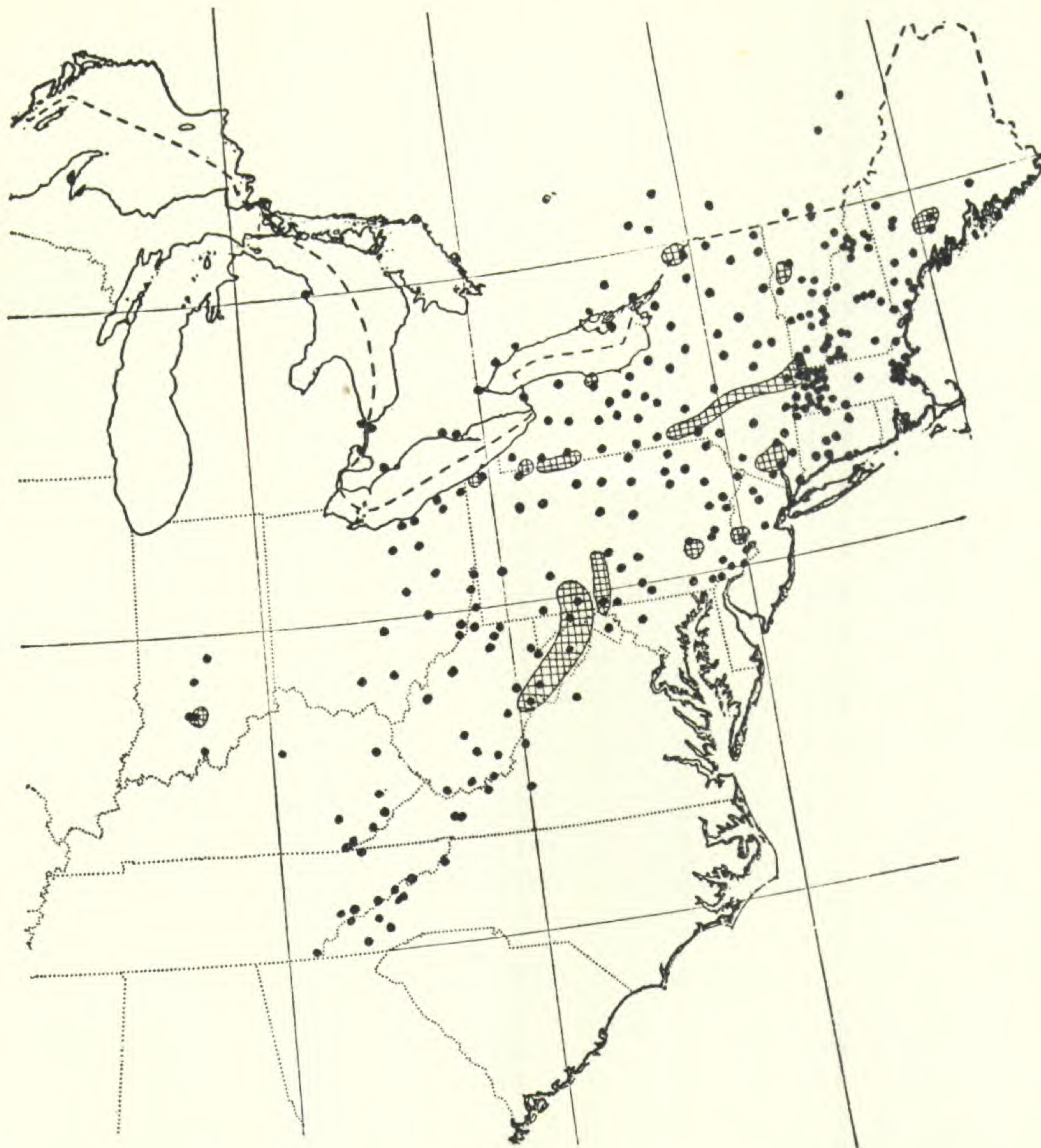
MAP 8. Differences between the Tuscarora region and other regions, derived from map 3.

MAP 9. Differences between the Schuylkill region and other regions, derived from map 3.



MAP 10

Differences between the Indiana region and other regions. The line of crosses represents the southern limits of glaciation; where this line splits, the southern part delimits Wisconsin glaciation and the northern part the earlier glaciations. The base map is Hall's Outline Map, 801M.



MAP 12

Cross-hatched areas: regions where mass collections of *R. odoratus* have been made. Dots: range (excepting Nova Scotia), based on collections in the Gray Herbarium, New York Botanical Garden, New England Botanical Club, New York State Museum, the Universities of West Virginia, Toronto, Pennsylvania, Kentucky, Cincinnati, Tennessee, and Wisconsin, the records of Dr. E. Lucy Braun and Dr. R. M. Harper, Schaffner's 'Ohio Vascular Plants,' and Deam's 'Flora of Indiana.' The base map is Hall's Outline Map, 801M.

MAP 13

R. parviflorus var. *genuinus*. Dots: range according to Fernald. X's: other collections.

MAP 14

R. parviflorus var. *hypomalacus*. Dots: range according to Fernald. X's: other collections.

MAP 15

R. parviflorus var. *heteradenius*. Dots: range according to Fernald. X's: other collections.

MAP 16

R. parviflorus var. *bifarius*. Dots: range according to Fernald. X's: other collections.

MAP 17

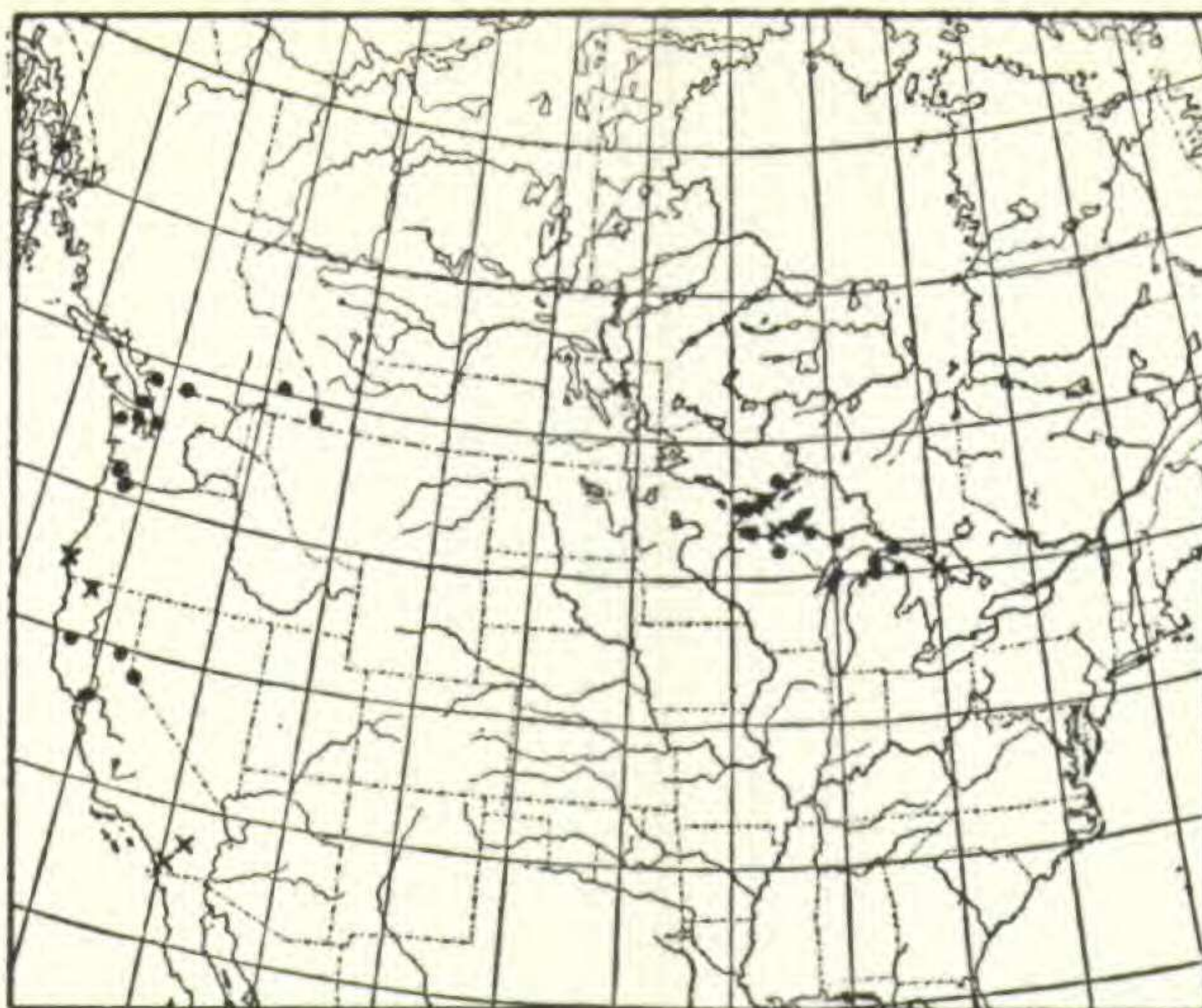
R. parviflorus var. *grandiflorus*. Dots: range according to Fernald. X's: other collections.

MAP 18

Dots: *R. parviflorus* var. *scopulorum*, and triangles, var. *parvifolius*, ranges according to Fernald. X's: other collections of these two varieties. Crosses: other collections of plants like them but with leaves velvety beneath.



13



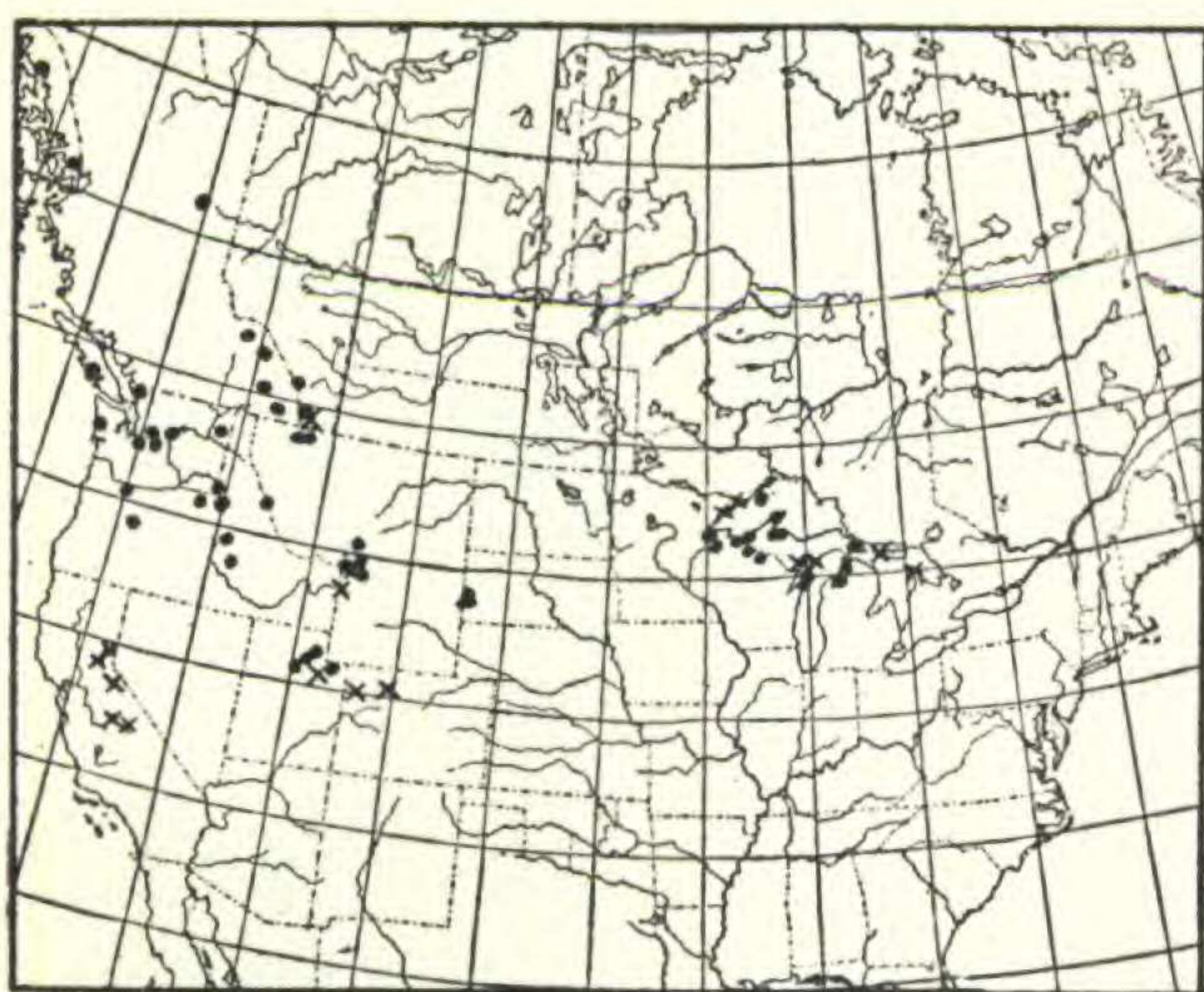
14



15



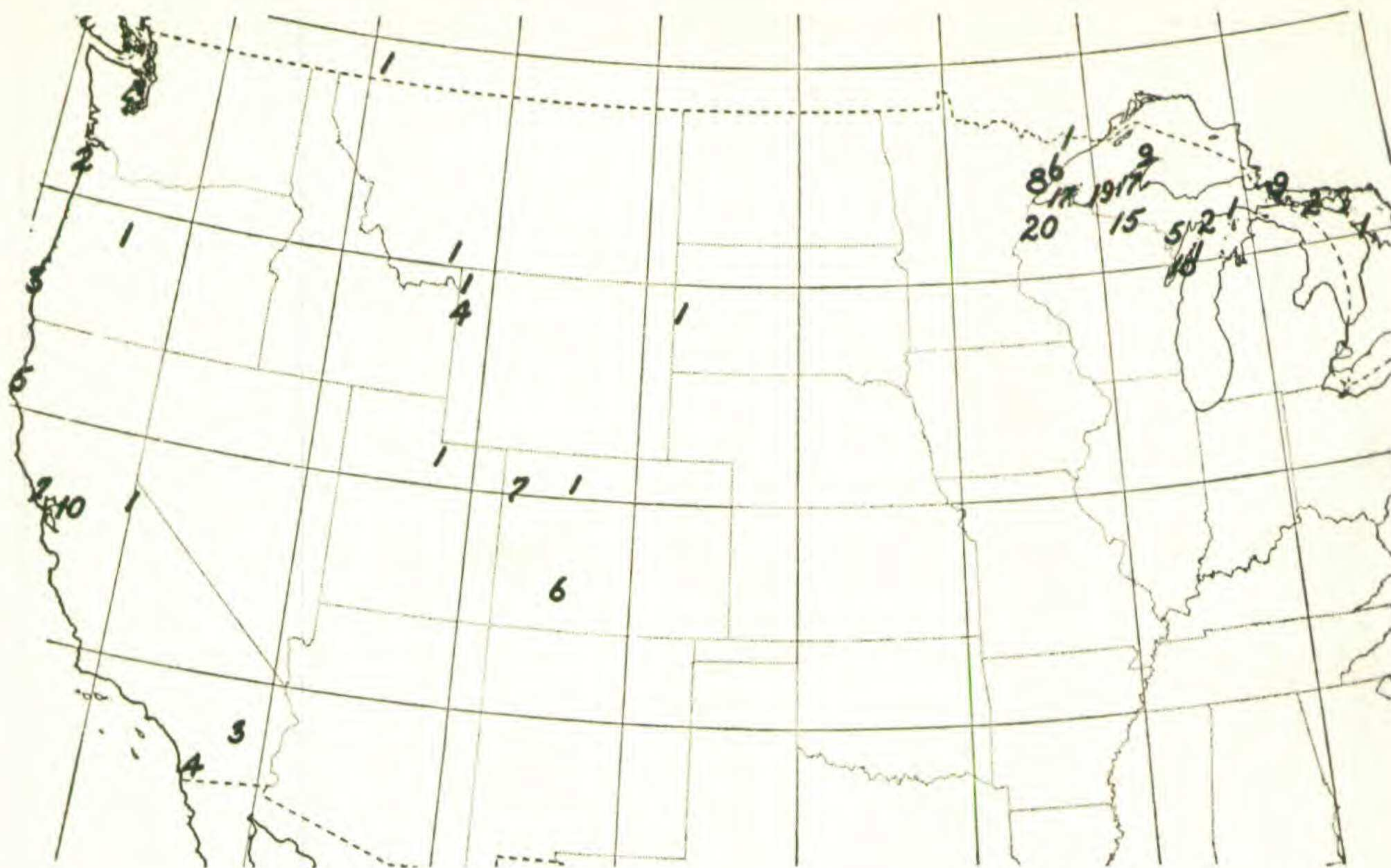
16



17



18



MAP 19

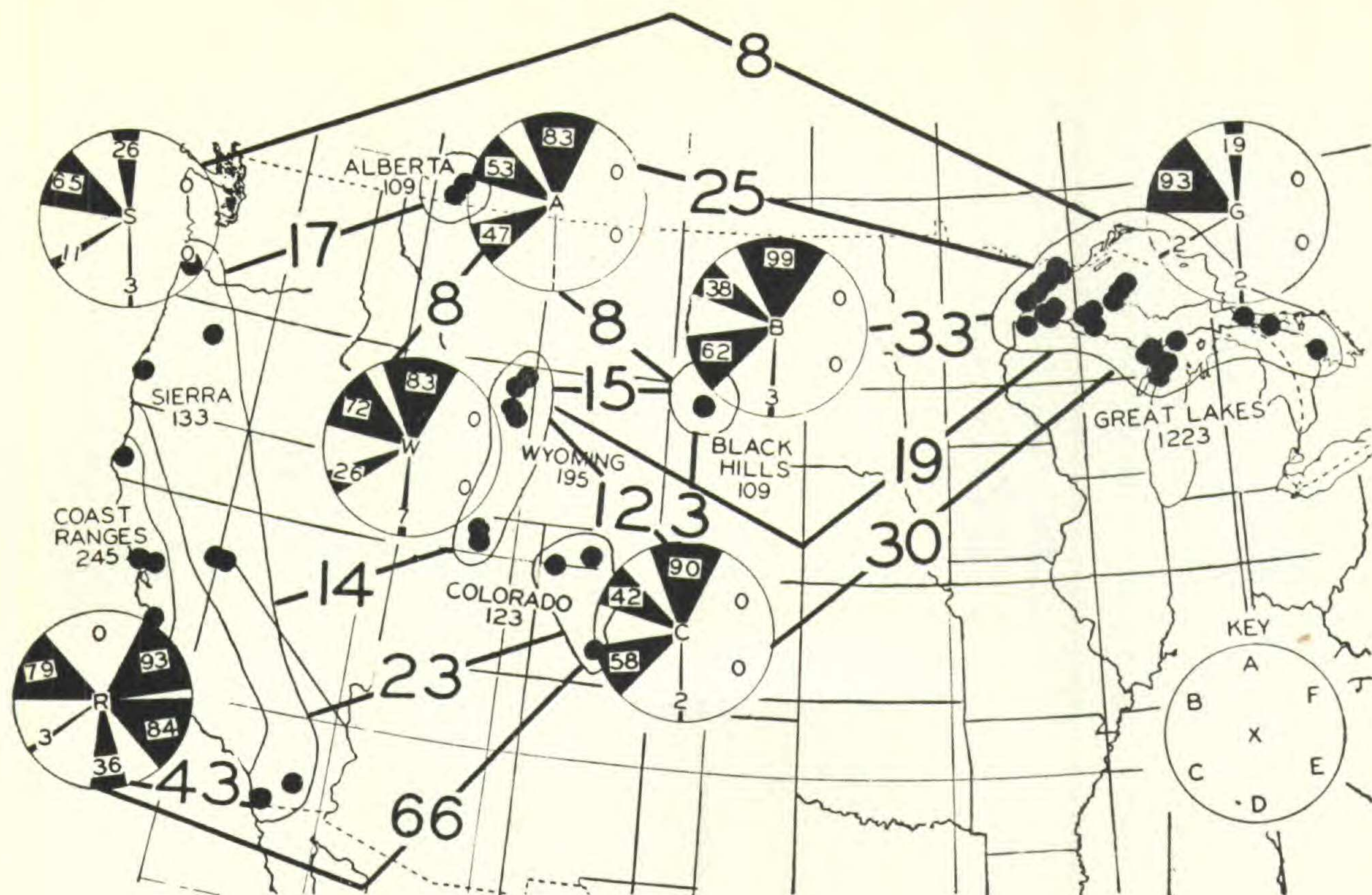
Slanted figures show locations of mass collections of *R. parviflorus*. A new series starts in each state or province, and figures missing indicate localities close to the locality bearing a lower number. The base map is Hall's Outline Map, 801M.

MAP 20

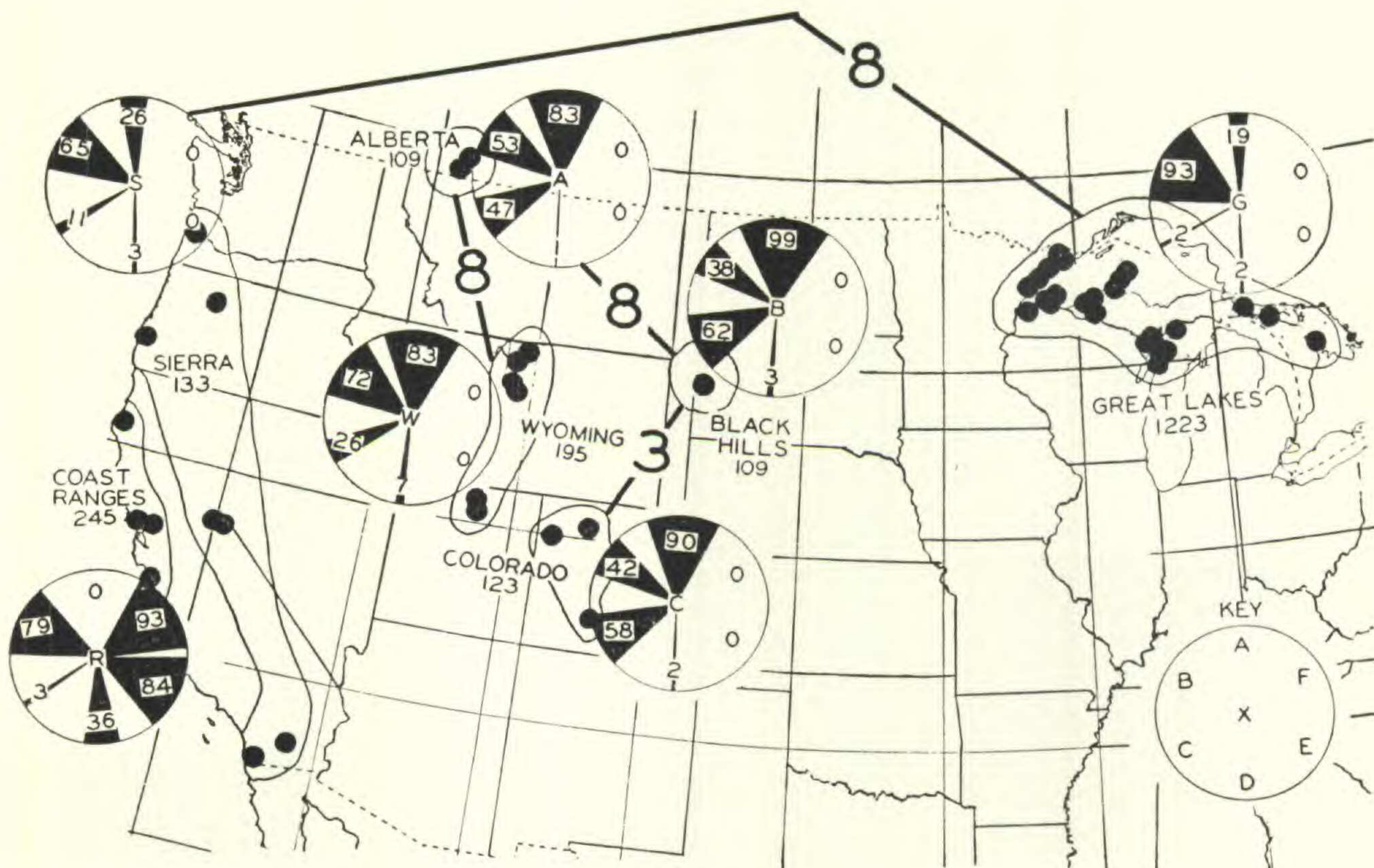
Stations where mass collections of *R. parviflorus* have been made (dots) grouped into regions (enclosed by lines). The figure below the name of each region indicates the number of individuals collected from that region. A pie-diagram for each region indicates in each sector the percentage of occurrence of a character as follows (refer to key): sector A, per cent of individuals with leaves glabrous or glabrate beneath; sector B, per cent with glands 0.5–1.0 mm. long on the pedicels; sector C, per cent with glands sessile or subsessile on the pedicels; sector D, per cent with villous calyx; sector E, per cent with villous pedicels; sector F, per cent with stem, stipules and petioles villous. In the center of each diagram (position X) is an initial referring to the name of the region. The average differences between regions (from table VIII) are shown by large figures on the heavy lines connecting regions.

MAP 21

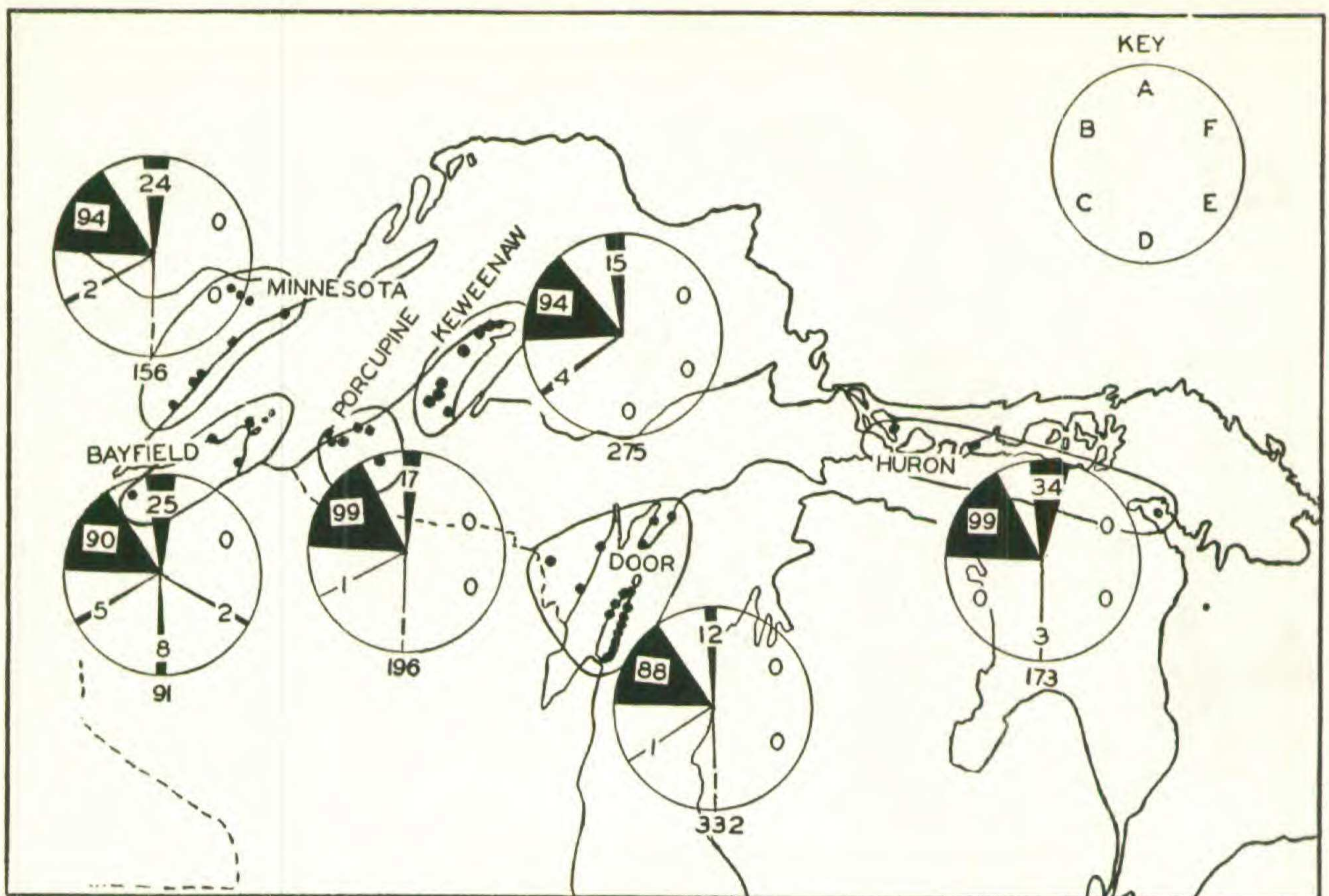
Differences less than 10. The base map for maps 20 and 21 is Hall's Outline Map, 801M.



MAP 20

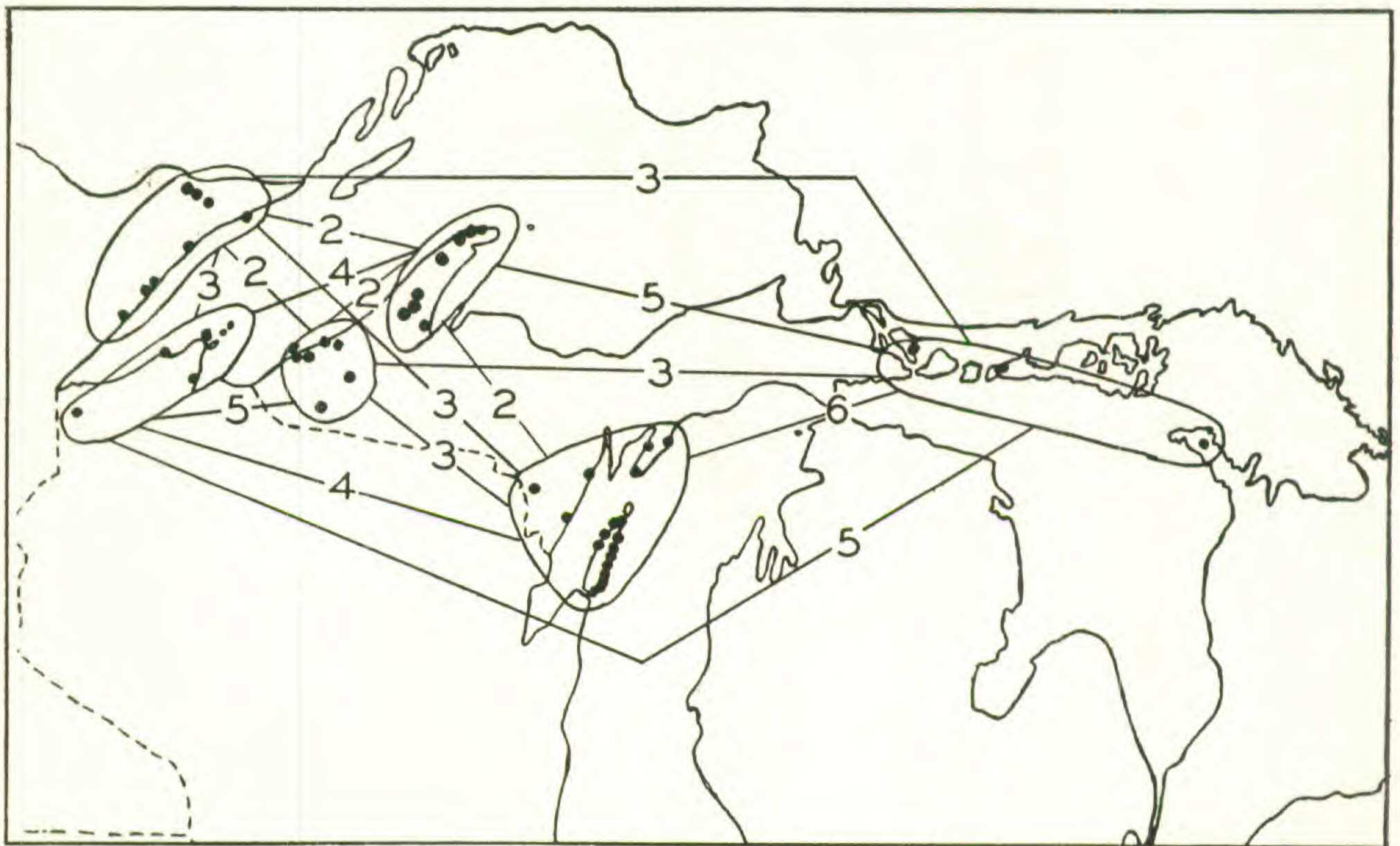


MAP 21



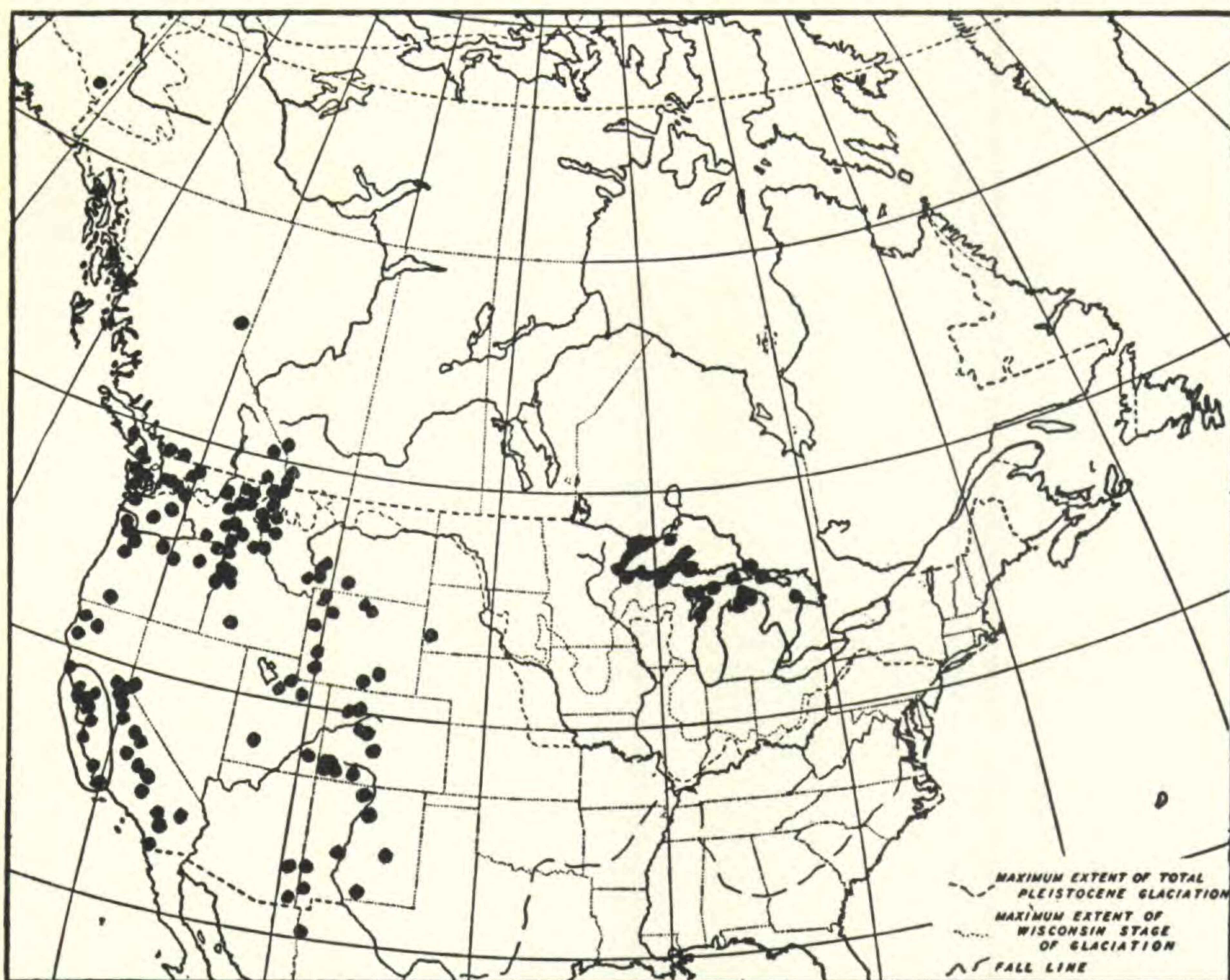
MAP 22

Stations about the Great Lakes where mass collections have been made (dots) grouped into regions (enclosed by ellipses). For explanation of pie-diagrams see caption under map 20. The figure below each pie-diagram indicates the number of individuals collected from that region.



MAP 23

Differences between regions about the Great Lakes, derived from map 22.



MAP 24

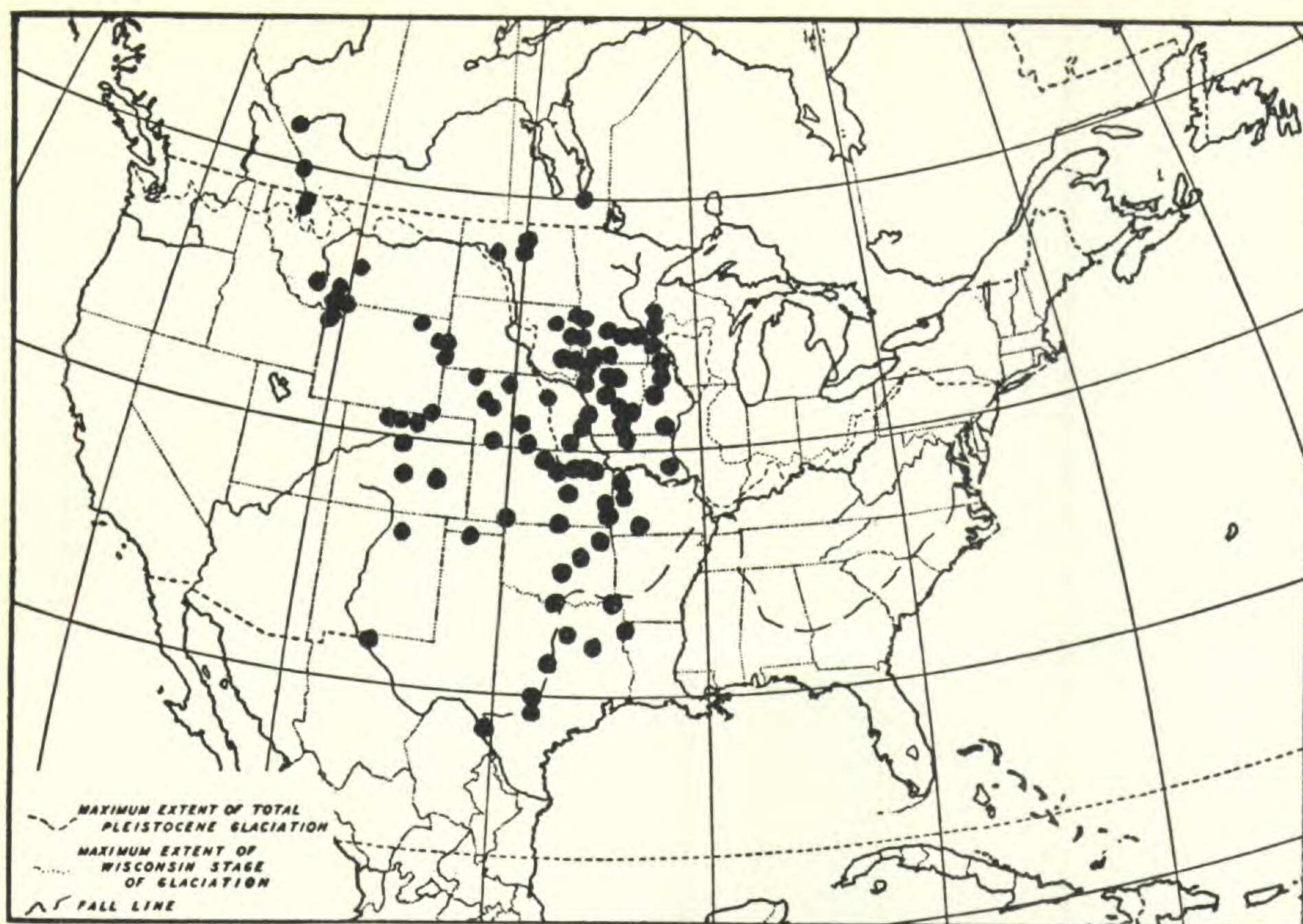
Range of *R. parviflorus*, and var. *velutinus* (in ellipse), from Fernald, *l.c.*, the Herbaria of the New York Botanical Garden, Pomona College, and the Universities of California and of Wisconsin, and letters from Drs. F. K. Butters and Hugh Raup. The base map is Hall's Outline Map, 205C, for maps 24, 25 & 26.

MAP 25

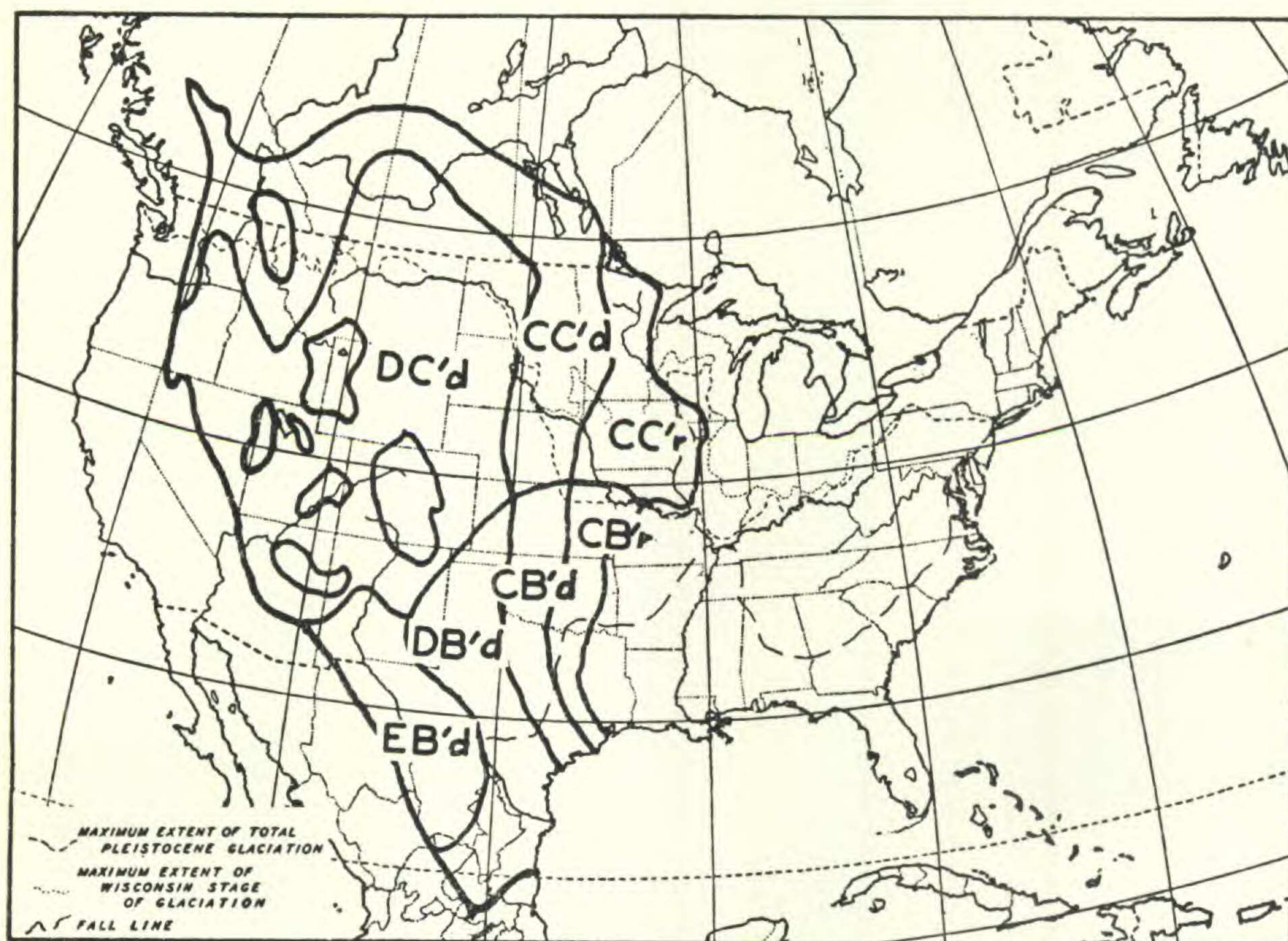
Range of *Astragalus caryocarpus*, from Fassett, 'Leguminous Plants of Wisconsin.'

MAP 26

The heavy lines enclose some of the climatic provinces described by Thornthwaite, Geogr. Rev. **21**, no. 4: *Pl. III*; the symbols describe the provinces as follows: C indicates subhumid, D, semiarid, and E, arid; B' indicates mesothermal and C' microthermal; r indicates precipitation adequate at all seasons, and d indicates precipitation deficient at all seasons.



MAP 25



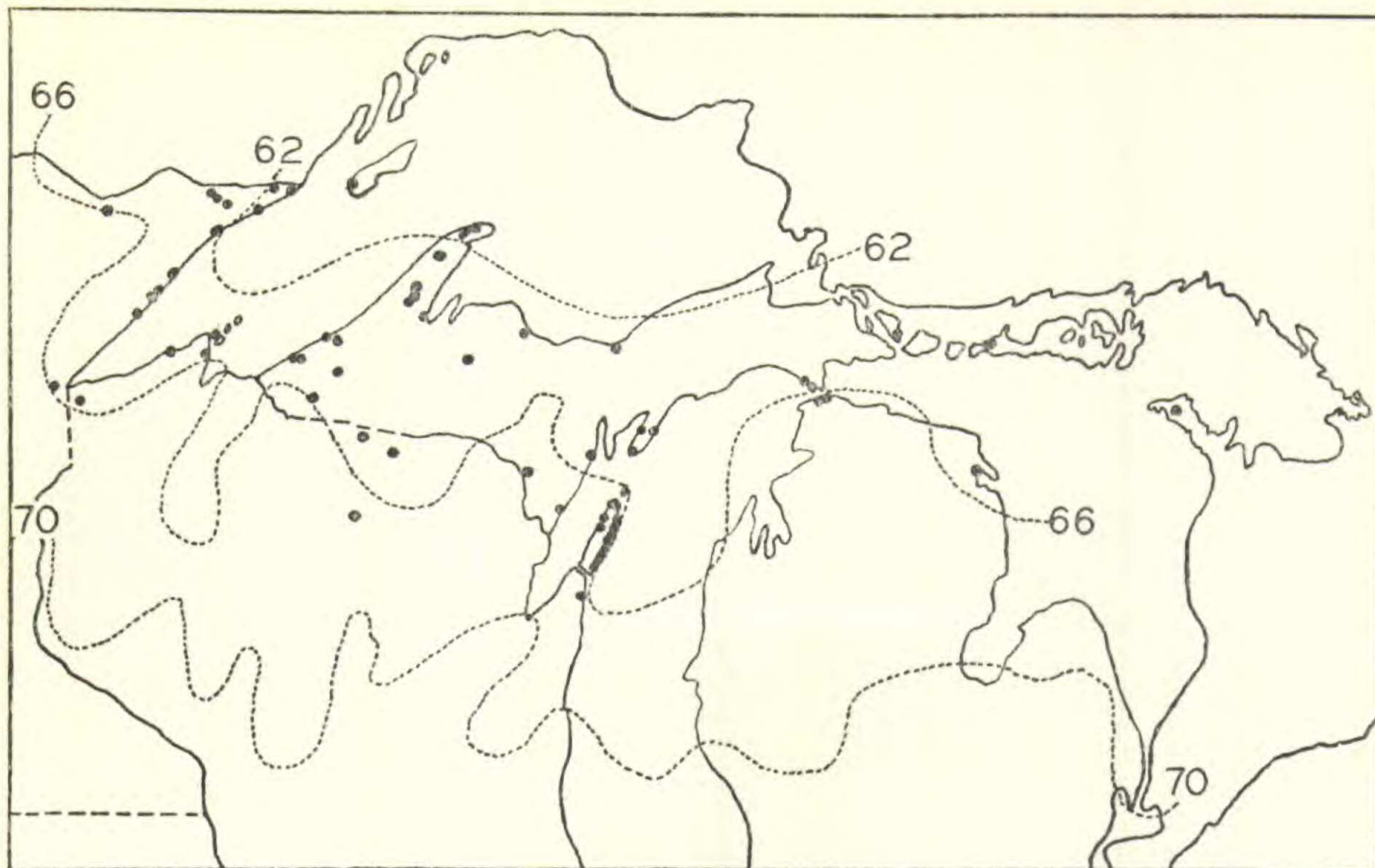
MAP 26

MAP 27

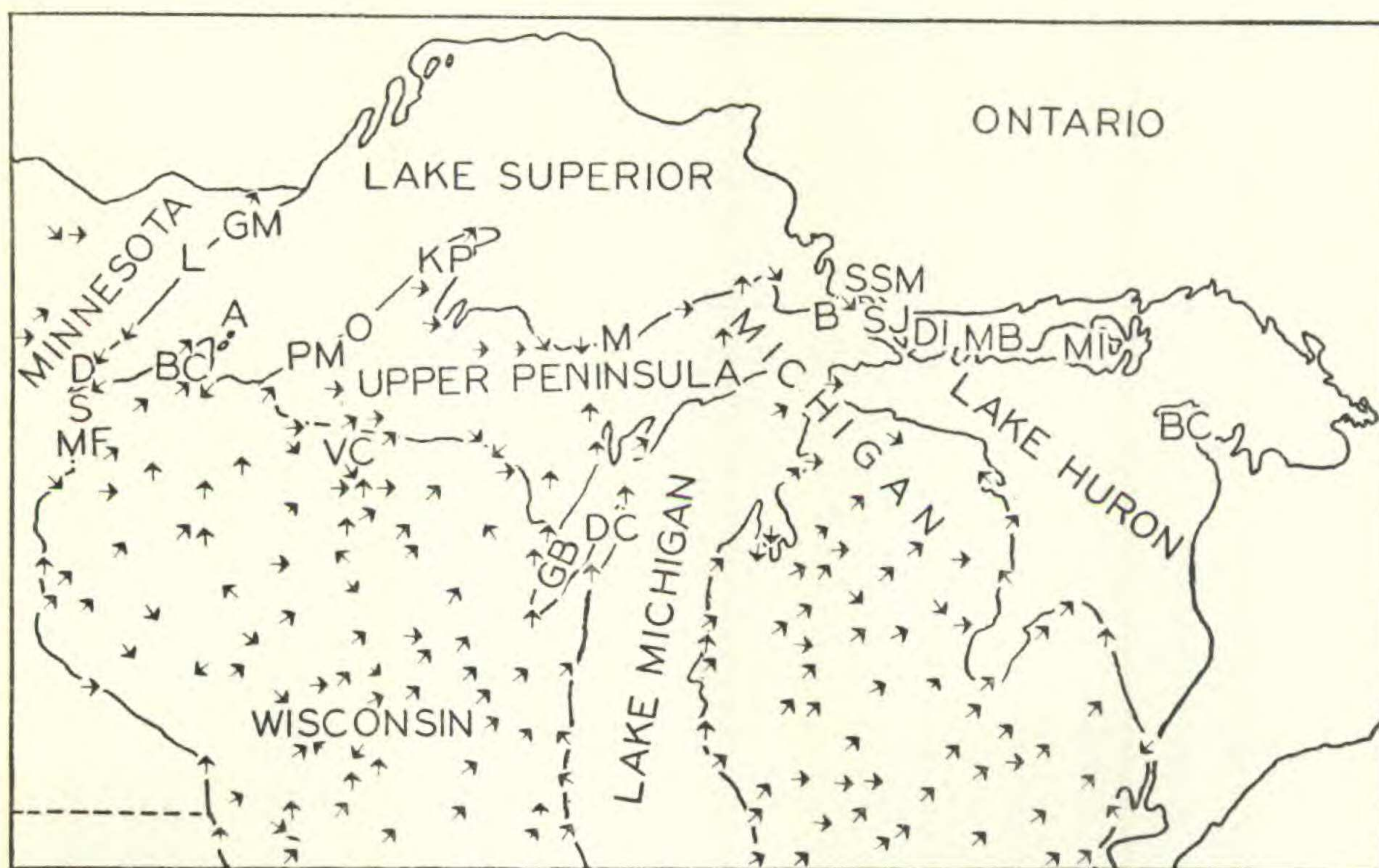
Dots: range of *R. parviflorus* in the Upper Great Lakes region. Dotted lines: isotherms for average temperatures for July, compiled from Sections 44, 45, 46, 47, 48, 49, 63, 64 & 65, "Climatic Summaries of the United States," published by the U. S. Weather Bureau.

MAP 28

Arrows show prevailing wind direction for July, compiled from "Climatic Summaries of the United States." Letters indicate places referred to in the text, as follows: A, Apostle Islands; B, Brimley; BC (in Canada), Bruce County; BC (in Wisconsin), Bayfield County; D, Duluth; DC, Door County; DI, Drummond Island; GB, Green Bay; GM, Grand Marais; KP, Keweenaw Point; L, Lutsen; M, Munising; MB, Meldrum Bay; MF, Manitou Falls; MI, Manitoulin Island; O, Ontonagan; PM, Porcupine Mountains; S, Superior; SJ, St. Joseph Island; SSM, Sault Ste. Marie; VC, Vilas County.



MAP 27



MAP 28

MAP 29

Range of *Populus balsamifera*, generalized from Munns, U. S. Dept. Agr. Misc. Publ. 287: 76. 1938. The base map is Hall's Outline Map, 205C, for maps 29-34.

MAP 30

Range of *Picea glauca*, generalized from Munns, *l.c.*, 35.

MAP 31

Range of *Arabis divaricarpa*, generalized from Hopkins, *Rhodora* 39: 131. 1937.

MAP 32

Range of *Arabis Drummondii*, generalized from Hopkins, *l.c.*, 138.

MAP 33

North American range of *Botrychium Lunaria*, generalized from Clausen, Mem. Torr. Bot. Club 19: 63. 1938.

MAP 34

Range of *Rubus parviflorus*, generalized from map 24 of this paper.



29



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31



32



33

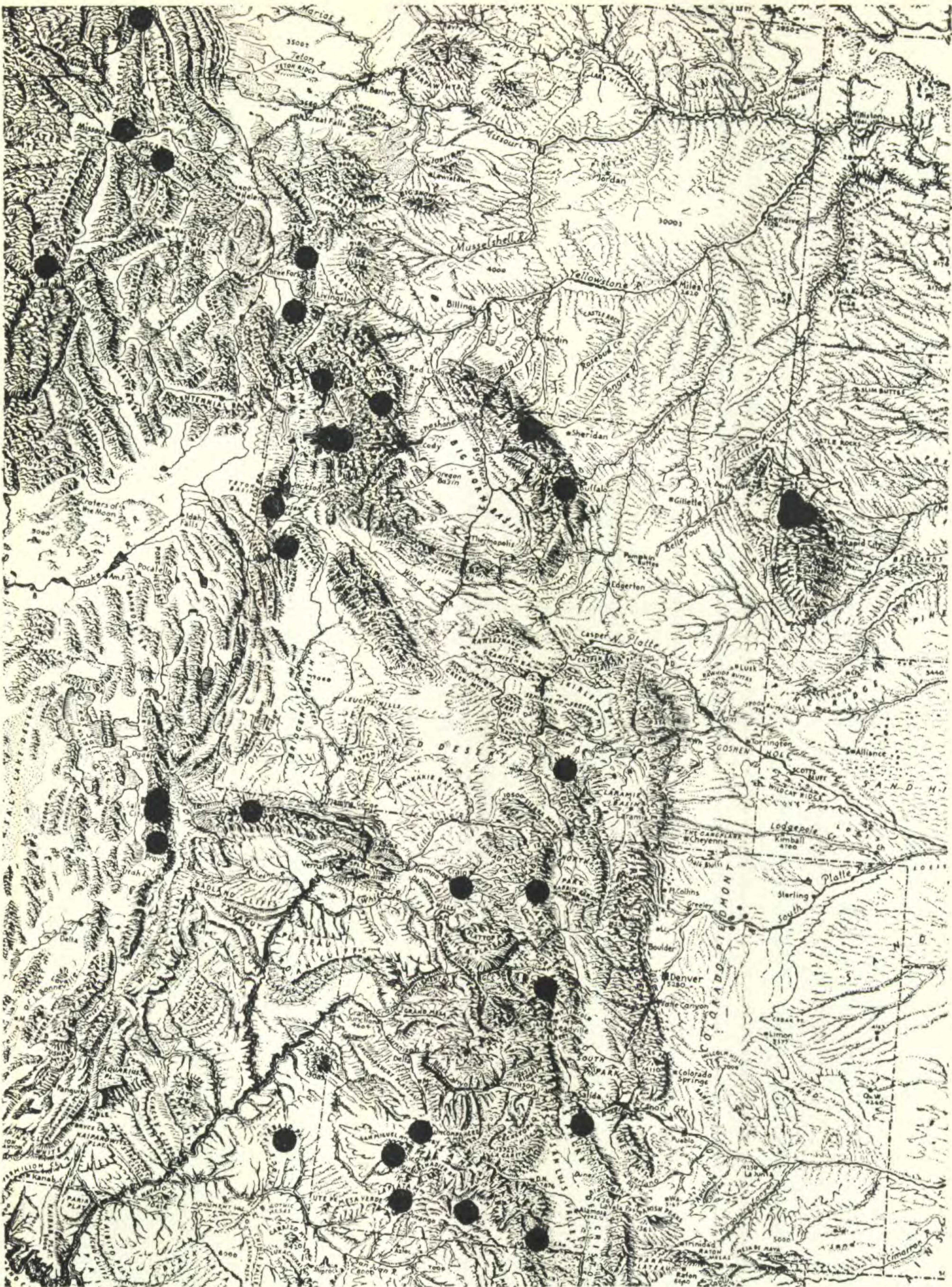


34



MAP 35

Range of *R. parviflorus* (solid black dots), *R. parviflorus* var. *velutinus* (half-black dots), and mixed colonies of the two (three-quarters-black dots), and their relation to topography in California and Nevada. Base map from Erwin Raisz in Atwood's 'Physiographic Provinces,' courtesy of Ginn & Co.



MAP 36

Relation of the range of *R. parviflorus* (dots) to topography in Wyoming, Colorado, and parts of adjacent states. Base map from Erwin Raisz in Atwood's 'Physiographic Provinces,' courtesy of Ginn & Co.

EXPLANATION OF PLATE

PLATE 9

Fig. 1. Thimbleberry occurring in solid growth along a roadway, and as scattered plants in adjacent woods, near Toivola, Michigan. This patch contains at least three of the so-called varieties of this species.

Fig. 2. Thimbleberry growing in an old lumbering road near Lutsen, Minnesota. At least three of the so-called varieties of *R. parviflorus* occur in this patch.



1



2

FASSETT—MASS COLLECTIONS: RUBUS

EXPLANATION OF PLATE

PLATE 10

Fig. 3. Thimbleberry as a fence-row plant in Mohawk, Keweenaw County, Michigan.

Fig. 4. Thimbleberry in the gorge below Fish Creek Falls, Steamboat Springs, Colorado. This patch contains at least four of the so-called varieties of *R. parviflorus*.



3



4

FASSETT—MASS COLLECTIONS: RUBUS

EXPLANATION OF PLATE

PLATE 11

Fig. 5. Mouth of Little Cottonwood Canyon, Salt Lake City, Utah. Photograph by Prof. Walter Cottam, University of Utah.

Fig. 6. City Creek Canyon, Salt Lake City, Utah. Photograph by Prof. Walter Cottam, University of Utah.



5



6

FASSETT—MASS COLLECTIONS: RUBUS

EXPLANATION OF PLATE

PLATE 12

Fig. 7. Little Cottonwood Canyon, Salt Lake City, Utah. Photograph by Prof. Walter Cottam, University of Utah.